Mechanische und elektrophysiologische Untersuchungen an Trichobothrien von Webespinnen (Agelenidae)

Dissertation

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Mechanics of Trichobothria in Orb-weaving Spiders (Agelenidae, Araneae)

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Summary. When a fly is humming at a distance of about one centimetre from an orb-weaving spider (Agelenidae) the trichobothria on the spider's extremities are deflected by air streams and air vibrations. Frequency analysis of the hum of the two prey animals, *Drosophila* and *Musca,* shows that the effective sound velocities of the harmonics with frequencies inferior to some five hundred Hz exceeds that of higher frequencies by a factor of at least 5. Biologically relevant resonances would, therefore, have to be looked for in the range of a few hundred Hz. Frequency response diagrams show that single hairs have no resonance between a few Hz and approximately 2 kHz. The maximal relative amplitude of hairs of different lengths shifts from the longer to the shorter hairs with increasing frequency. As this is only a minor effect, however, it appears that there is no frequency discrimination by the mechanical apparatus. Constant air streams with a velocity of 40 mm/s cause hair deflection of about 10 degrees (the hair's bend is neglibible). Similarly, near-field particle velocity of sound fields up to a few hundred Hz is well transmitted. The mechanical directional sensitivity does not depend on the azimuthal angle of deflection. Thus, information about direction and velocity of stationary and near-field air movements is transmitted without deformation by the mechanical apparatus. This is well matched with the fact that the hair is multiply innervated.

Introduction

The trichobothria on the extremities of Araneae were discovered by Dahl (1883) and have been subject to several phases of research since then. Their morphology was studied by Görner (1965, light microscopy), Emerit (1967, innervation) and Christian (1971, 1972, electron microscopy). The biological function of the trichobothria was investigated as well. Dahl called them "Hörhaare" (hairs of hearing) without offering a more precise definition of the term. Hansen (1917) thought that they had the function of a tactile sense organ. In behavioural experiments Görner and Andrews (1969) showed that a blinded *Agelena* is able to seize vibrating dummy preys by precisely determining position and direction. Thus the term "Ferntastsinnesorgane" (distance tactile sense organs) coined by Dijkgraaf (1947) seemed to be applicable to the trichobothria. Further behavioural experiments (Görner and Reißland, unpublished) revealed, however, that dummy preys can be seized even after elimination of all trichobothria. This behaviour is, presumably made possible by slit sense organs (cf. Barth, 1972) which are always excited by air vibration in the trichobothria's range of biological function. Reaction readiness diminishes, however, after elimination of the trichobothria.

The present paper attempts to describe the dynamic properties of the trichobothria's stimulus transmitting structures. The point in question is to find out and evaluate the parameters of air flow that are likely to provide clues at the corresponding biological information processing. Electrophysiological description of the trichobothria receptors will be submitted in the following paper.

Material and Methods

Specimens, males and females, of the common house spider *Tegenaria derhami* (Scopoli), *Tegenaria atrica* (C.-L. Koch) and of the spider *Agelena labyrinthica* Clerck in their last moulting stages were used. Measurements were partly carried out on the animal in vivo while it was fixed on its support by means of insect needles.

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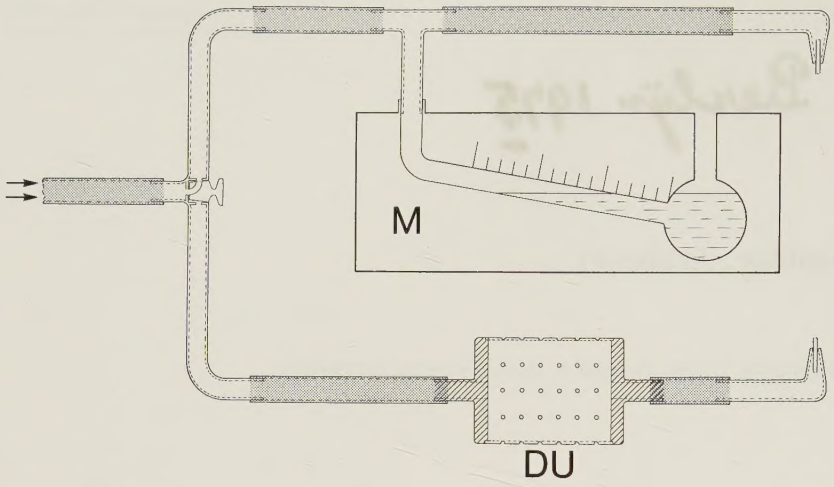

Fig. 1. Arrangement for generation of slow air stream. Air from left (arrows) issuing from compressed-air bottle; either directed to one nozzle (upper one) for pressure measuring or to the other nozzle for the experiment. *M*, manometer; *DU*, pressure reducer; manometer filling: heptan ($\rho = 0.6898$ g/cm^3)

The spider was mostly placed on a black velvet cushion in order to get a dark background for observation.

The remaining measurements were performed at the spider's leg freshly autotomized at the trochanter. The leg's proximal end was generally sealed with vaseline. The experiment had to be carried out within an hour, for after this interval the mechanical properties changed. An animal could lose several legs without further visible signs of damage.

1. Measurements in Stationary Air Stream

The trichobothrium was placed close to a nozzle through which a weak air stream emanated from a compressed-air bottle. The inner diameter of the nozzle, which consisted of a capillary glued to the inner walls of the glass tube, amounted to 1105 µm. Thus, compared to the length of the hairs of less than 600 µm, it was sufficiently wide to invite the supposition that the hair was exposed to an air stream of constant velocity.

The velocity of air emanation was measured indirectly. At a given air pressure, the volume Δv that emanated from the nozzle within a minute was measured. Be f the cross-section surface of the nozzle then

$$\frac{\Delta v}{\Delta t} = f \cdot \frac{\Delta x}{\Delta t}.$$

From that equation the emanation velocity $\Delta x/\Delta t$ could be calculated. In the experiment, the static air pressure served as a measure for the calculated air stream velocity. Since the positive air pressure was very small the individual measurements were preceded by measurements of the positive air pressure by means of a modified U-tube manometer (Fig. 1). The air stream was then diverted by a cock and lowered by the factor 1/49. The remaining air stream was used for trichobothrium deflection. The lines for measurement of pressure and deflection angle were equal-dimensioned. Frictional losses between manometer and emanation nozzle were negligible.

2. Frequency Analysis of Flight-Sound of Flies

The airborne flight-sound of *Musca* and *Drosophila* was recorded by means of condenser microphone and tape-recorder. It was analyzed with a wave analyzer HP 3590A at a filter width of 10 Hz. (Measurements were carried out in the Heinrich Hertz Institut für Schwingungsforschung in Berlin. Our thanks are due to Dr. Börger for his generous help.)

3. Comparison of Resonance Properties of Different Hairs

At a distance of 10 cm from a loudspeaker a living adult *Tegenaria* was so fixed on a small cushion that tarsus and metatarsus of one leg protruded into space parallel to the direction of sound propagation. Deflection of the trichobothria on the tarsus was measured under the binocular microscope. With loudspeaker position unaltered the corresponding hair to be measured was moved to a certain point in the binocular's object plane. Sound particle velocity was adjusted in such a way that the hair farthest deflected had a definite amplitude ($\leqq 10$ deg, cf. Görner, 1965) with each frequency adjusted.

For technical reasons amplitude-frequency response for low frequencies (range of 1–100 Hz) was recorded in the sound near-field (flow field) and for higher frequencies in the far-field (vibration field). This distinction is irrelevant for the trichobothrium which, certainly, is no pressure receptor. In principle, a hair can react to movement only, and its far field function can, therefore, only reside in measuring the velocity of air particle (Autrum, 1942, 1963; Markl, 1973).

4. Measurements in Sound Far-Field

For producing a definite sound field a loudspeaker was connected to a square tube (brass) the free end of which, in order to avoid reflection, was closed by a long rock-wool wedge (cf. Fig. 2). Dimensioning was such as to make sure that the distance between loudspeaker and open tube end was about $\lambda/4$ corresponding to the sound frequency of 150 Hz. Thus it was guaranteed that at frequencies exceeding this limit no reflection could occur. Prior to measuring, the sound pressure in the region of the experimental object was calibrated by means of a capacitor microphone inserted through the tube's side. Frequencies lower than 150 Hz gave rise to error because the object support and the calibrating hole were not at the same place. The estimated error always amounted to less than 2%.

The object support consisted of a rotable rod (diameter 3 mm) protruding into the tube's interior at a distance of 5 cm from the loudspeaker membrane. A plate holding the rod in position was flanged to the tube's bottom side. A freshly autotomized leg of a spider was fixed to the rod's flat end.

The leg was exposed to sound waves parallel to its longitudinal or transversal axis. For determination of the mechanical directional sensitivity a pointer to the rod and a protractor were used, both

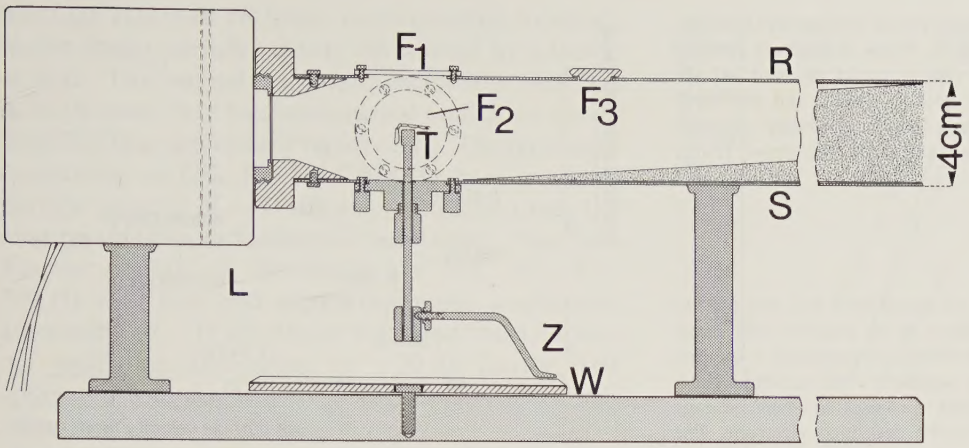

Fig. 2. Device for measuring amplitude-frequency response and mechanical directional sensitivity of trichobothria in sound field. *L*, loudspeaker; *R*, brass square tube (l = 65 cm); *S*, rock-wool wedge for sound absorption; *T*, rotatable object support and spider leg; *Z*, pointer; *W*, angle scale; F_1 and F_2, lucite windows for object observation; F_3, opening for sound pressure calibration. Amplitude measuring through F_1

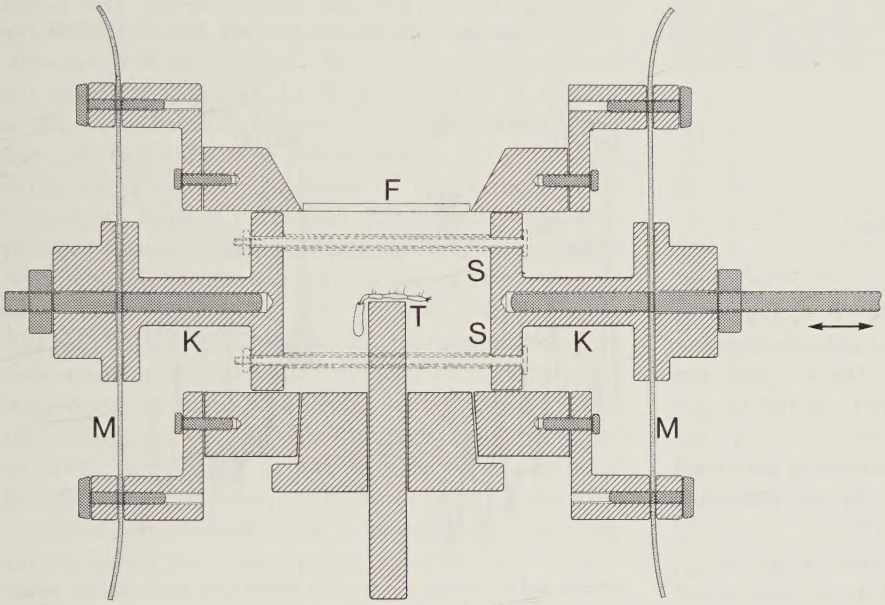

Fig. 3. Device for generation of sound near-field. *K*, pistons, rigidly connected by brass rods *S*; *M*, rubber membrane; *T*, rotatable object support and spider leg; *F*, glass window for observation. Central right rod connected to loudspeaker. Sine wave oscillation quality stroboscopically controlled by observation of oscillation form both of piston and trichobothrium

of which allowed adjustment of azimuthal angle of the leg segment. The movements of the trichobothria could be observed from above through a binocular microscope or from the sides through lucite windows in the tube's walls. In order to keep amplitude measuring errors as small as possible the hair amplitude was kept constant whereas the sound pressure was adjusted correspondingly. This allowed serial measuring up to the kHz-range. Sound particle velocity within the whole range of measurements was unphysiologically high (an effective sound particle velocity of 11 mm/s corresponds to about 100 phon).

5. Measurements in Sound Near-Field

For hair deflection at very low frequencies a lucite tube closed at both ends by rubber membranes was used. In the tube's interior two pistons rigidly connected by bars were moved harmonically back and forth by a loudspeaker (cf. Fig. 3). This arrangement was responsible for generating a sine-shaped air flow corresponding to an ideal sound near-field.

In the middle of the tube the object was fixed on a lucite rod (diameter 4 mm) in compliance with the arrangement in the one-side-open tube. The trichobothrium was observed from above. Since the piston device displayed signs of hysteresis piston stroke and hair deflection were measured two by two through two binocular microscopes at every individual frequency adjusted. Loudspeaker amplitude had a definite predetermined value. Phase response was determined as follows. A stroboscope (Philips PR 9107) was triggered by the sine wave voltage fed into the loudspeaker. Both the sine wave and the stroboscope discharge signal appeared on an oscilloscope. The binocular microscope provided standing pictures of both piston and trichobothrium. Then the stroboscope

discharge phase was so shifted that the piston's image was precisely in the middle of the deflection region. Phase differences between piston movement and sine wave voltage could be read off the oscilloscope. Phase shifts between trichobothrium and sine wave voltage were determined analogously. Phase differences between piston and hair were arrived at by subtracting the above results from each other.

6. Measurements in Vacuum

A rotatable object support with a plasticine head was mounted to a lucite table. The object was pinned to its support with insect needles. With a lucite hood put over the arrangement a vacuum of some torr could be achieved by means of a Minnipumpe (Leybold) and a water jet pump connected in row. A sine-wave voltage of $40\ V \leqq U_{pp} \leqq 1\ kV$ was applied to the deflection electrode. The object support served as counter electrode. Since the hair generally charged positive it was thrown into vibration by the alternating field (Görner, 1965).

Experimental objects were either an intact spider, which survived evacuation of the vessel during measurement (some min) undamaged, or an autotomized leg sealed airtight with "Uhu plus 5 Minuten". Without hermetic sealing the haemolymph issued and the trichobothria were deformed so that measurement could not be finished to completion.

Results

1. Trichobothrium Deflection and Bend in Stationary Air Stream

When a humming fly is held close to a *Tegenaria* or *Agelena* at a distance of about 1 cm, observation through a binocular microscope shows that the spider's trichobothria in the proximity of the fly are deflected to one side and generally oscillate in that new position. A first phase of investigation consisted in finding out the velocities of air stream necessary for the deflection of the trichobothria.

The deflection of 2 trichobothria of an intact house spider is shown in Figure 4 as a function of stationary air stream velocity. The curves give an impression of the order or magnitude of biologically relevant air currents on which a trichobothrium is capable to react. A deflection of 5 degrees of a hair of medium length (400 µm) requires a stream velocity of about 10 mm/s. This demonstrates that trichobothria are extremely sensitive to air movement. Action potentials occur at deflection angles $\gtrsim 3$ degrees (cf. the following paper).

For comparison, Figure 4 contains amplitudes of some trichobothria measured in the sound field of 100 Hz (abscissa: effective sound particle velocity). Figure 4 also includes a value measured at a trichobothrium of comparable length of a *Tegenaria* long dead. Since the basis was completely stiff (cf. also Section 9) this value provides information about the hair's bend.

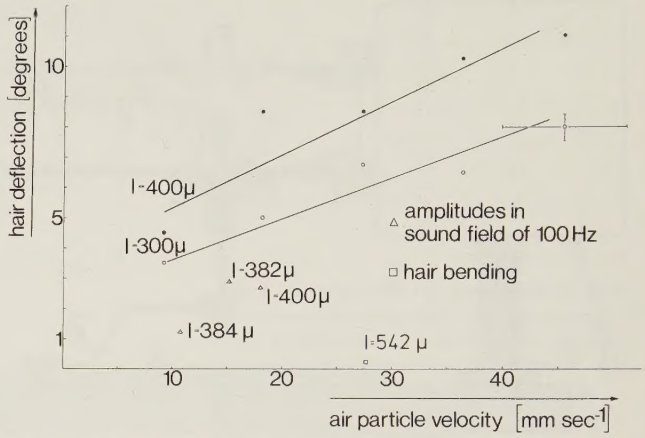

Fig. 4. Deflection and bending of trichobothria in laminar air flow. Fitting curves for uniform flow are drawn according to visual estimate; bars indicate variation range of air velocity and angle data. The values for 100 Hz oscillations were measured in sound far field (Fig. 2), their abscissa values indicate effective sound particle velocity of air. All hairs were more or less bent. Their lengths were measured as a straight line from the basis to the hair top

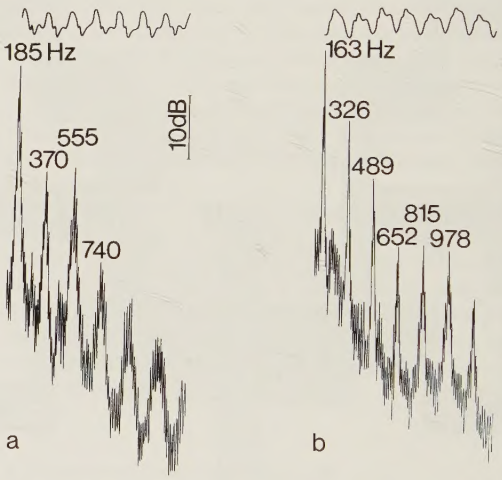

Fig. 5a and b. Fourier spectrum of sound field generated by *Drosophila* (**a**) and *Musca* (**b**). Filter width of frequency analyzer is 10 Hz. Pressure differences measured in dB equal differences in sound particle velocity. Above each spectrum picture of original oscillation

2. Sound Frequency Spectrum Analysis of Musca and Drosophila

Since in the investigated spider species flies are a common prey the order of magnitude of the frequency contents in the hum sound of flies had to be determined. For this purpose the airborne sound resulting from the beat of wings of *Musca* and *Drosophila* was analyzed (cf. Williams and Galambos, 1950; Sotavalta, 1963; Esch and Wilson, 1967). The results are shown in Figure 5. The fundamental oscillation of *Musca* amounts to 163 Hz. The first harmonic oscilla-

tion (326 Hz) is 10 dB lower corresponding to an effective sound particle velocity diminished by a factor of 0.32. The second harmonic oscillation (489 Hz) is 20 dB lower than the fundamental oscillation corresponding to a diminishing factor of 0.1. The harmonic oscillations of 652, 815, and 978 Hz have a sound particle velocity of −31 dB only, i.e., 0.03 times the amount of the fundamental oscillation. The first Fourier partials of *Drosophila* are 185, 370, 555, 740 Hz with first and second harmonic oscillations amounting to −15 dB (factor 0.18) and third harmonic oscillation amounting to −30 dB (factor 0.03 compared with the velocity of the fundamental oscillation).

3. Trichobothria Deflection as Function of Their Topography

Trichobothria on the tarsus of 4 *Tegenaria* and 3 *Agelena* were investigated. The frequencies used varied within a range of 10 Hz to 2.5 kHz. A typical result is presented in Figure 6. The amplitudes of the hairs are normalized to the amplitude of the farthest deflected hair. At a frequency of 10 Hz the longest hair shows farthest deflection; the shorter hairs' amplitudes show progressive decrease. With frequencies becoming higher the curves change so that the hair of medium length has the greatest amplitude at 320 Hz. With frequencies further increasing the curve maximum moves farther to the left. Thus, with varying frequencies hairs of differing lengths are deflected differently. As hair length increases from proximal to distal the spiders would be able to discriminate frequencies by comparing the amplitudes of different oscillating trichobothria if it is assumed that they are equipped with appropriate receptor cell connections.

Comparison of measurements of hair deflection in stationary air stream with those in sound field of corresponding particle velocity shows that the values in the sound field are not substantially inferior to those in uniform stream (cf. Fig. 4). A difference must be there for two reasons: (1) the hair's movement causes frictional losses at the basis and (2) the hair is not directly coupled to the air. The experiments demonstrate, however, that the hairs at any rate possess great movability (cf. also Figs. 8 and 9).

4. Deflection by Small Vibrating Disc

Measurements of the relative deflection of trichobothria of differing lengths had been carried out by placing each hair to a point the co-ordinates of which had been kept constant relative to the loudspeaker. Since a possible prey, however, may change its position relative to the spider and, moreover, since its sound field is less homogeneous than that of the loudspeaker the oscillation form of a hair during deflection was measured by means of a near-field more similar to that of a fly. For this purpose, a small vibrating disc with a diameter of 2 mm was used. Figure 7 contains the results of two different distances between disc and top of the hair and two different positions relative to the hair. The small disc oscillated harmonically with a frequency of 68.5 Hz. The oscillation form of the hair was measured by stroboscope.

When the small disc vibrates above the hair's top the trichobothrium oscillates at push-pull. The oscilla-

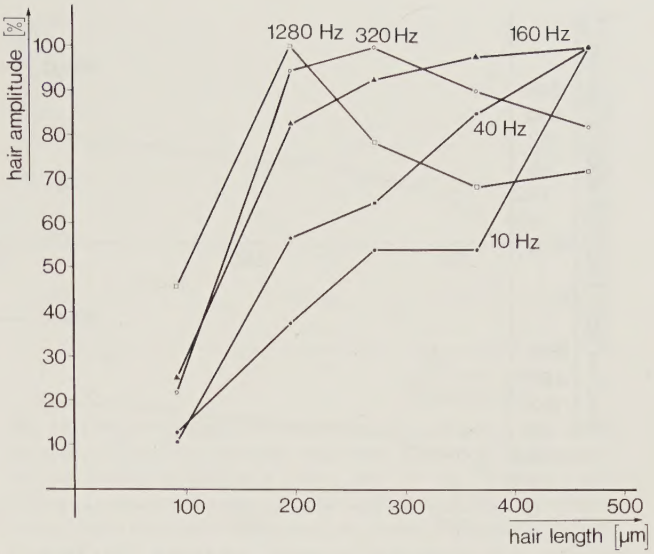

Fig. 6. Trichobothria deflection in sound field as a function of hair lengths, intact spider. Frequency as parameter. *Tegenaria*, tarsus of fourth right leg. Curves are normalized to oscillation width of greatest hair amplitude

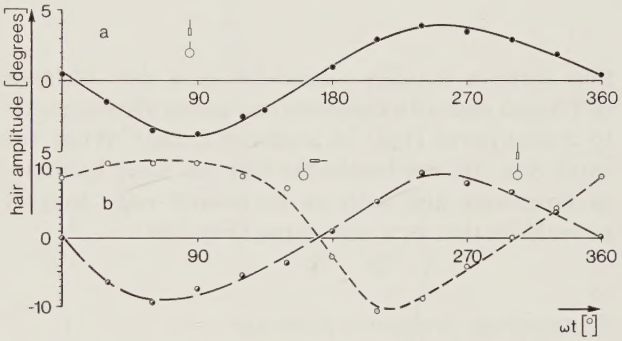

Fig. 7a and b. Oscillation form of trichobothrium at stimulation by means of harmonically oscillating small disc (diameter 2 mm, peak to peak amplitude 0.925 mm). Position of disc with regard to trichobothrium illustrated by insets. Distances hair top−disc edge amounted to 2 mm (**a**) and to 1.5 mm (**b**), respectively. Circuit frequency $\omega = 430.4$ Hz, hair length 500 µm

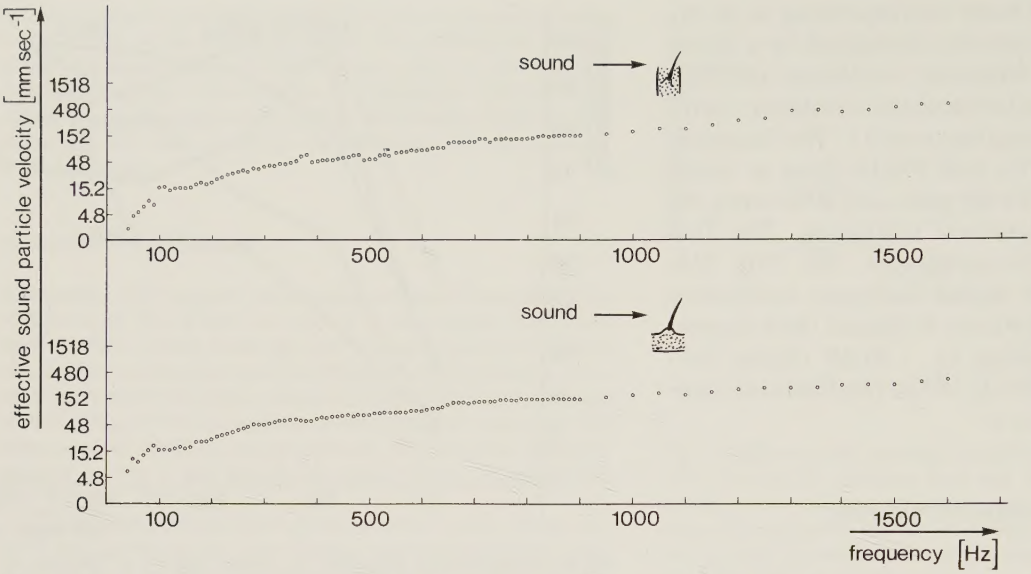

Fig. 8. Amplitude-frequency response of trichobothrium at two different azimuthal angles, measured in sound far-field. Insets illustrate position of leg limb relative to direction of sound propagation. Loudspeaker amplitude was adjusted as to bring about peak to peak amplitude of 4.7 deg. Ordinate indicating sound particle velocity required. *Tegenaria*, first leg right, metatarsus, second trichobothrium from distal of median row, 1 = 183 μm

tion form is roughly sinusoidal at a disc distance of 1.5 mm and with distances increasing grows similar to a sine curve (Fig. 7a, distance 2 mm). When the small disc vibrates beside the hair the latter oscillates in synchrony and with an oscillation only roughly resembling that of a sine curve (Fig. 7b).

5. *Amplitude-Frequency Response at High Sound Particle Velocities*

8 trichobothria of Tegenaria were deflected at frequencies from 40 Hz to a maximum of 1.6 kHz. In some experimental objects deflection to proximal as well as deflection transversal to the leg limb were measured. No significant differences were found (cf. Section 9). Figure 8 shows a typical frequency response. With exposure to sound waves transversal to the leg no relative minima indicating resonances were found. Other measurement curves exhibit similar results.

6. *Amplitude- and Phase-Frequency Response at Low Sound Particle Velocities*

a) Amplitude-Frequency Response. For 11 different trichobothria amplitude-frequency responses were recorded at frequencies between 5 and 100 Hz. In ten cases the hair was deflected longitudinally to the limb. Transversal deflection was brought about only once.

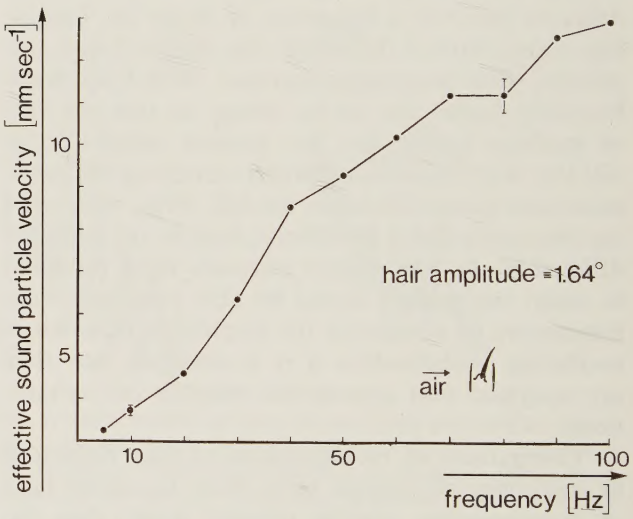

Fig. 9. Amplitude-frequency response at low frequencies, measured in sound near-field. Vertical bars indicate variation range of measurement values for sound particle velocity. *Tegenaria*, second leg right, metatarsus, first trichobothrium from distal of median row, 1 = 255 μm

Ten measurement series were performed with hair amplitudes being constant and four with piston amplitudes constant. The measurement results of one hair are graphically rendered in Figure 9. For bringing about a hair amplitude of 1.64 deg the sound particle velocity at 100 Hz must have 4 times the value than that at 5 Hz. The curve has a nearly linear increase. Significant minima corresponding to resonances do not occur.

b) Phase-Frequency Response at Low Frequencies. Deflection of four hairs transversal to the longitudinal axis of the leg limb was achieved at frequencies between 10 and 140 Hz. One result of phase measurement is shown in Figure 10: Curve c oscillates with small variation range near −30 deg. Phase shift does not occur. The result confirms the non-existence of resonances up to 140 Hz.

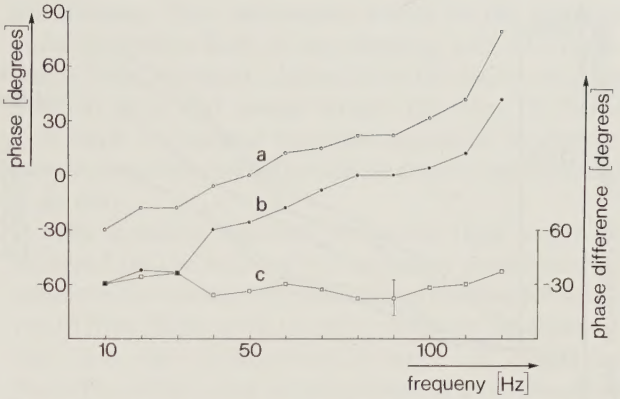

Fig. 10. Phase-frequency response at low frequencies. Curve *a* (left ordinate): phase shift between sine-wave voltage of loudspeaker and mechanical oscillation of piston pair (cf. Fig. 3), curve *b* (left ordinate): phase difference between voltage and hair movement, curve *c* (right ordinate): difference from *a* and *b*. *Tegenaria*, female, third leg right, metatarsus, second trichobothrium from distal of median row, l = 327 µm

7. Mechanical Directional Sensitivity

The mechanical directional sensitivity was determined by various methods. The most precise method turned out to be hair deflection in a sound field and it was carried out in accordance with the arrangement presented in Figure 2. 30 trichobothria of *Tegenaria* and 8 of *Agelena* were measured at a given frequency (f = 100 Hz and 300 Hz, respectively). Mechanical directional sensitivity both in *Agelena* and *Tegenaria* is nearly isotropic (Fig. 11a). Only in 9 out of a total of 38 hairs investigated the mechanical directional sensitivity was slightly flattened with respect to the axial direction of the extremity (Fig. 11b). This flattening is most probably due to the distal bend of the trichobothria and their correspondingly loser coupling to the air stream in direction of the leg's longitudinal axis.

8. Effective Hair Velocity as Function of Frequency at Different Directions of Deflection

The question had to be answered whether the dynamic properties of hair suspension change in accordance with the direction of deflection. For movements longitudinal and transversal to the axis of the leg limb this is not the case as is demonstrated in Figure 8. With view to their dynamic directional sensitivity 3 trichobothria were investigated in the tube (Fig. 2) between 100 Hz and 150 Hz (Fig. 12). Frequency response of effective angular velocity is plotted for different angles of deflection. Directional sensitivity is arrived at by reading the points of the different curves at a given frequency. It should be noted that there are only minor differences indicating a certain asymmetry in the elastic properties of the basis membrane or a slight damping effect depending on direction. All the curves have in common that there are no resonances whatever.

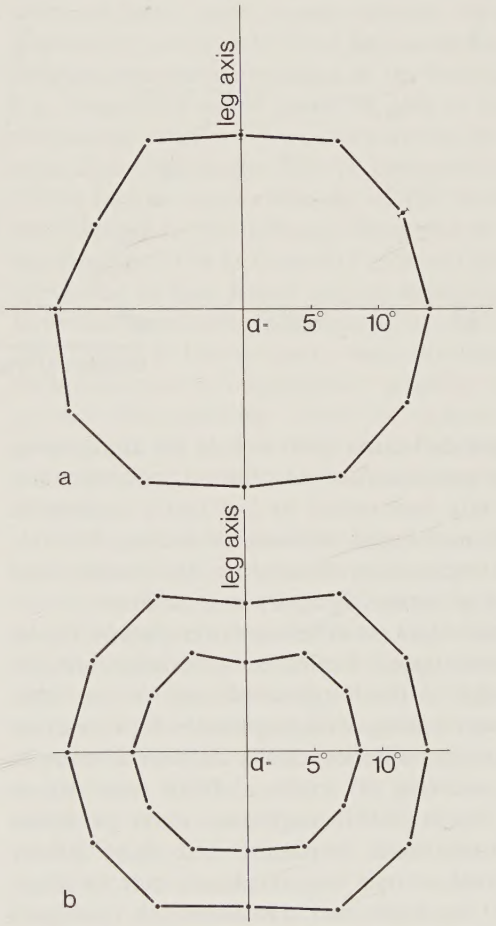

Fig. 11a and b. Mechanical directional sensitivity, measured in sound far-field at 300 Hz (**a**), at 300 Hz and 1280 Hz (**b**). *Tegenaria*, female, metatarsus, second trichobothrium from distal. l = 287 µm (**a**), l = 300 µm (**b**). Vertical bars indicate standard deviations of angle reading, calculated from 3 to 5 single values. Missing bars tantamount to standard deviation inferior to measurement points

9. Amplitude-Frequency Response at Electrostatic Deflection in Vacuum

Contrary to deflection in a sound field, deflection in vacuum is not impeded by air friction neither with

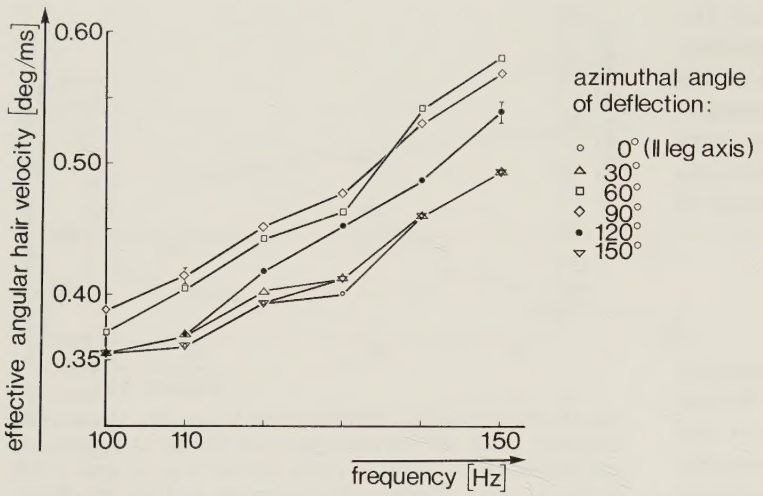

Fig. 12. Effective angular velocity of trichobothrium as a function of frequency at deflection in various directions. Zero degree corresponds to deflection parallel to leg axis. Sound pressure level and consequently sound velocity constant from 120 to 150 Hz; slight deviation of values at 100 and 110 Hz were corrected by computation. Amplitude 7.6 deg, kept constant. Vertical bars indicate variation range. *Tegenaria*, second leg right, metatarsus, l = 267 µm

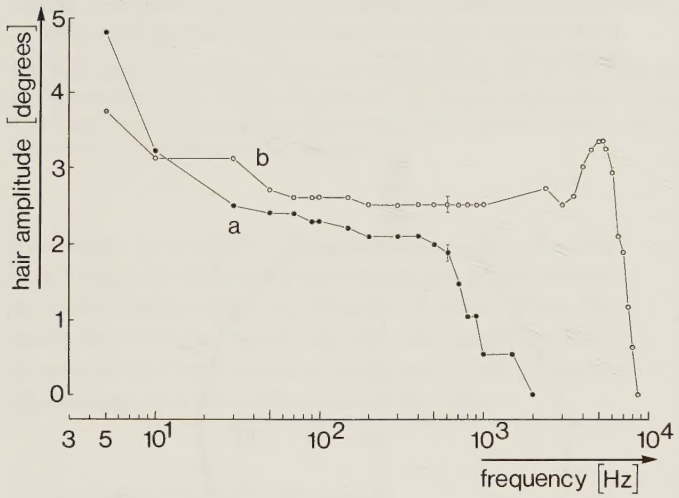

Fig. 13. Amplitude-frequency response at electrostatic deflection in vacuum (p = a few torr). Measurement up to about half an hour (*a*), measurement beginning about one hour after leg separation (*b*). *Tegenaria atrica*, female, second hair from distal, l = 550 µm

regard to the deflection itself nor as far as damping phenomena are concerned. Oscillation properties are, therefore, only determined by the hair's suspension at the basis and by its moment of inertia. Possible resonances presumably blurred in the sound field would have to appear distinctly in a vacuum.

10 trichobothria on different extremities of *Tegenaria* were investigated. Deflection was always brought about parallel to the longitudinal axis of the limb. At a sine-wave voltage with amplitudes kept constant the oscillation amplitudes mostly decreased monotonously to zero (Fig. 13, curve a) from some Hz to some kHz. Up to 100 Hz amplitudes never fell below half of the maximum amplitude, and up to 500 Hz they decreased to only one third as a rule (a single instance of one tenth was measured). In two cases frequency response was determined by adjusting the voltage in such a way that the hair amplitude remained constant. The resulting curves resembled a parabola.

When amplitude-frequency response was measured on the isolated leg which had been in vacuum for more than an hour the result differed from that measured under physiological conditions, i.e., intact spider or freshly separated, well-sealed leg. In the kHz-range trichobothria oscillation was substantially

Table 1. Trichobothria resonances on the tarsus of *Tegenaria*, female, measured in vacuum about 1.5 h after separation of the leg. Electrode position ensured deflection parallel to leg limb axis. A different position would have engendered resonances slightly modified

Number of hair from distal	Length	Resonance at	Shortened to	Resonance at
1	510 µm (broken off)	2.0 kHz	220 µm	3 –3.15 kHz
2	520 µm	1.8 kHz	250 µm	3.8–3.9 kHz
3	470 µm	3.1 kHz	230 µm	7.1–7.2 kHz
4	410 µm	3.5 kHz		
5	360 µm	4.7 kHz		
6	260 µm	4.2 kHz		

stronger (Fig. 13, curve b). Resonances occur in this range, e.g., in curve b at 2.5 and 5 kHz. These resonances depend on the hairs' lengths as is shown in Table 1 giving a comparison of resonances for 6 hairs of differing lengths. The resonances were determined by manual sweeping the sine-wave voltage. Resonances were doubled when the hairs were shortened by about one half of their original length.

Discussion

The extreme sensibility of trichobothria to slight air movements was already noticed by Dahl (1883). They can, therefore, easily be distinguished from the rigid tactile sensilla (cf. Foelix and Chu-Wang, 1973).

Behavioural experiments indicated that trichobothria play a role in locating prey (Görner and Andrews, 1969; Görner and Reißland, unpublished). Here the question arises whether unipolar flow, periodically alternating flow (acoustic near-field), far-field sound particle velocity or air turbulences are exclusively or primarily evaluated. Investigation of the mechanical properties of trichobothria, therefore, constitutes a first attempt at finding an answer to this question.

Trichobothria receptors will begin to discharge at a hair deflection of about 1 degree (cf. Görner and Andrews, 1969, and succeeding paper). Amplitudes in this range can only be achieved in an acoustic far-field with sound particle velocities to which a spider in natural environment will hardly be exposed to. The corresponding categories of sound amount to about 90 phon. The fact that far-field sound particle velocity can, therefore, not be regarded as an adequate stimulus is in good agreement with the following observation. A prey object cannot be seized unless it moves within an area of about 1 cm around the spider. In this case, the uniform and near-field flow by far outweighs the far-field sound particle velocity.

It is remarkable that the bend (cf. Fig. 4) only amounts to about 3% of the deflection (relative to the deviation of the hair's top from the resting position) and is, therefore, within the limits of error of biological signal processing. This property has the effect that the input stimulus is transmitted to the receptor cells with great effectivity. This finding may, possibly, differ from the measurement results obtainable from an intact animal, since it cannot be excluded that the hair's mechanical properties change with age. Stiffening of the hair shaft would ameliorate, stiffening of the hair suspension would deteriorate stimulus transmission.

There are several possible mechanisms for detection and, possibly, recognition of a prey causing air disturbances. One mechanism would be the analysis of the oscillation form of the vibrating hair. The oscillation form, however, depends on the hair's relative position to a real sound source (cf. Fig. 7). Thus, it is hard to imagine that the organism is able to extract any utilizable information about a prey animal from that.

The question whether the sound field might be analyzed on the basis of its frequency spectrum was attempted to answer by different experiments. Analysis of flies' flight-sound could give rise to the expectation that the trichobothria's range of sensitivity should be of the order of magnitude of a few hundred Hz, since frequencies exceeding about 500 Hz involve sound particle velocities that amount to less than a fifth of the sound particle velocities of the fundamental oscillations (cf. Fig. 5).

If it is assumed that trichobothria are suitable instruments for evaluating periodical air movements with regard to frequency contents, then either some hairs, at least, must possess several resonance frequencies or every individual hair must have a single definite resonance frequency in the biological range. E.g., long hairs would better be able to react to low frequencies whereas short hairs would be able to do so at high frequencies. This is, obviously, what Dahl (1911) had in mind. Because of the trichobothria's small length (a few 100 μm) compared to the sound wavelengths to be evaluated ($\lambda \gtrsim 20$ cm) no resonance effect due to hair length can be expected. It might, however, be possible that the stiffness of hair suspension varies. If this property was correlated with the trichobothrium's topographic position again frequency discrimination could be achieved. Experiments indicate that relative hair amplitude indeed shifts to shorter hairs when frequency is increased (Fig. 6).

There are two plausible objections to these measurements which can, however, be rejected. (1) The resonance effect is not brought about by possible frequency-dependent interferences, i.e., changes in the sound field at the place of measuring, because similar results are obtainable in the tube (cf. Fig. 2). (2) The resonance effect is not caused by frequency-dependent changes of friction or turbulence parallel to the longitudinal axis of the spider's leg because amplitude-frequency response is almost independent of the azimuthal angle of deflection (cf. Figs. 8 and 11b).

Since it is shown (Figs. 8, 9, 10 and 12) that the frequency-dependent relative maxima of the hair amplitudes are also not traceable to resonances of the individual hairs it may be concluded that the reduction in hair amplitude as a function of increasing frequency has different slopes depending on hair lengths: With low frequencies longer hairs will have

higher amplitudes. If reduction in amplitudes of shorter hairs is superior to that of longer ones their ratio would at a certain frequency fall below 1. Thus, the relative maxima of the shorter hairs will occur at frequencies higher than the frequency mentioned.

The change of relative amplitude in several trichobothria of a single leg limb measured in a field of an even sound wave is probably of no biological relevance, for this effect would be concealed by local flow potential gradients occurring in natural fields. Contrary to that, possible resonances of single hairs could more easily be utilized by the organism.

In hair amplitude measurements (Figs. 8, 9, 10 and 12) it must be taken into consideration that possible resonances of the system may perhaps be blurred because air friction has a damping effect. For it is the trichobothria's rough surface (Christian, 1971) which guarantees optimal air connection and therefore impedes occurrence of excessive amplitudes. Measurements in vacuum (Fig. 13) prove, though, that in the frequency range of prey, i.e., up to some kHz, resonances of the hair definitely don't occur. Only at a few kHz resonances can be found. Here, obviously, the resulting oscillation properties were essentially determined both by the hairs' moment of inertia and by the elasticity of suspension, while damping is strongly reduced. Responsible for this is presumably the desiccation of the cells at the basis of the bothrium and possibly of the membrane.

Thus, the question wether the sound field is analyzed with respect to its harmonic partials must, as far as the dynamic hair properties are concerned, clearly be answered in the negative. Are trichobothria, then, no "hairs of hearing" as Dahl (1883, 1911) assumed?

Obviously, this question cannot be answered satisfactorily unless the anthropomorph term "hear" is adequately defined for invertebrates. Trichobothria are certainly no "hairs of hearing" in the sense Dahl had in mind, i.e., longer hairs perceive lower and shorter hairs higher frequencies. From the point of view of perception of sound—even if restricted to near-field sound—however, they could be "hairs of hearing" judging from the mechanical properties of the trichobothria's external auxiliary structures (cf. also Haskell, 1956; Drašlar, 1973; Wiese, 1976). In contrast to both trichobothria arranged on the cerci of insects (Nicklaus, 1965; Gnatzy and Schmidt, 1971; Bischof, 1975) and trichobothria on the pedipalps of scorpions (Hoffmann, 1967) the mechanical directional sensitivity of the trichobothria of Agelenidae is isotropic (Figs. 11 and 12, cf. also Smola, 1970). The trichobothria of spiders have at least three receptors (Görner, 1965; Christian, 1971, 1972) reacting to hair deflection in various directions. Their flexible suspension in the bothrium allows perception of any stimulus direction (cf. also Haupt, 1970, 1975; Haupt and Coineau, 1975).

From our experiments, therefore, we may conclude that it is probably the direction and the velocity of extremely weak, uniform air currents as well as sound near-field in the frequency range of prey that appears to be evaluated by the spider. These informations are obviously well conveyed by the stimulus transmitting apparatus both because of good coupling to air due to the hairs' pinniform build and their very elastic suspension. The transducing receptor properties will be described in the following paper.

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Electrophysiology of Trichobothria in Orb-weaving Spiders (Agelenidae, Araneae)*

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Summary. Trichobothria of the house spiders *Tegenaria atrica* (C.L. Koch) and *Tegenaria derhami* (Scopoli) were stimulated by linear deflection of the hair from its resting position to one side. The pulse response of the receptor cell was analyzed. At angular deflection velocities of $10^{-2} \leqq \omega \leqq 1$ deg/ms the receptor begins to discharge at an angle of $\alpha \approx 3$ degrees. While the mean pulse rate remains constant during deflections of $10^{-2} \leqq \omega \leqq 10^{-1}$ deg/ms the pulse train may be interrupted by repeated breaks. Discharge continues when the hair is bent proximally beyond the bothrium edge. When the hair is bent distally and touches the bothrium edge, however, discharge ceases. Responsible for this phenomenon seems to be an asymmetry of hair suspension. – Repeated deflection leads to logarithmically ascending latency curves and logarithmically falling curves of the pulse numbers. The function coefficients depend on velocities and repetition rates of the deflections. The adaptational effect is heightened by preceding stationary deflection in the direction of the dynamical stimulus. The mean pulse rate as a function of hair deflection velocity increases logarithmically. The mean pulse rate as a function of hair movement direction obeys a cosine law, provided that a given velocity and a definite deflection angle are used.

Introduction

The question of what is a sense organ's biological relevance can, principally, be answered by behavioural experiments only. As for the trichobothria of Agelenidae Görner and Andrews (1969) conclude that their function is correlated to the location of vibrating objects of prey. As mechanical investigations have shown the stimulus transducing apparatus of the sensilla is able to convey almost undeformed certain signals inherent in temporarily changing air movements. These are the velocity of air stream or the sound particle velocity of the near field up to frequencies of several hundred Hz and the stream direction component parallel to the leg surface (Reißland and Görner, 1978). The question arising then is how a single receptor makes use of the information arriving. The answer to this question implies the treatment of problems such as (1) to which angles of deflection does a receptor respond to; (2) how does it react to simple hair deflection; (3) how quickly does adaptation occur; (4) what deflection velocities are discriminated and (5) what kind of mechanical directional sensitivity can be found. Some of these items were already investigated by Görner (1965). It is possible, within certain limits, to draw inferences about what information the organism evaluates by means of the trichobothria (cf. Mountcastle, 1967; Perkel and Bullock, 1968) from the receptor's transducing properties.

The second aspect of the experiments was of receptorphysiological nature. This was the question of what can be inferred about the receptor's functioning from the temporal pattern of response (cf. Grundfest, 1975). For comparison, investigations on the cuticular mechanosensilla of other arthropodes (Nicklaus, 1967; Gnatzy and Schmidt, 1971; Barth, 1972; Gaffal and Hansen, 1972; Gnatzy, 1972; Schmidt, 1972; Risler, 1972; Drašlar, 1973; Ottoson, 1974; Thurm, 1974; Thurm et al., 1974; Barth and Pickelmann, 1975; Bischof, 1975; Gaffal et al., 1975; Gaffal, 1976; Rick et al., 1976) and studies on other mechanoreceptors (Nakajima and Onodera, 1969a and b; Loewenstein, 1971) were used.

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Material and Methods

1. Experimental Objects

Experimental animals were *Tegenaria derhami* (Scopoli) and *Tegenaria atrica* (C.L. Koch) both males and females. The spider was anaesthetized with CO_2 and fixed on its support by means of insect needles. A black velvet cushion served as a support to get a dark background for the observation. Prosoma, opisthosoma and every single leg were so pressed to the support by means of needles that the animal was hardly able to move. The spiders generally survived the experiment for some hours.

2. Recording

Recordings were carried out from the sensilla of the tibia of the pedipalpus by means of a capillary electrode with a large opening (about 100 µm). The electrode touched the cuticular surface of the patella (cf. Görner, 1965). The pedipalpus was supported by needles and its end attached to needles by means of wax colophony. Recordings were mostly carried out from the third or fourth hair of the upper row (counted from proximal to distal) and occasionally from one of the lateral sensilla (cf. Görner, 1965). The remaining trichobothria and all neighbouring bristles and pinniformed hairs were removed with fine pincers. Signals of the slit sense organs (cf. Barth, 1973) were also received by the recording method described. The slit sense organs, however, responded only to high sound pressure levels or to substrate vibrations, phenomena which generally did not impede the recording operations.

3. Trichobothria Deflection

Reproducible hair deflection was achieved by means of a loudspeaker (basket diameter 5 cm) to the membrane of which a thin aluminium rod (diameter 2 mm, length 8 cm) was sticked to. A second membrane made of hard plastic (thickness 0.5 mm) mounted on the loudspeaker held the rod centrically and strongly damped the mechanical system. This membrane was required for keeping as small as possible the overshooting due to abrupt returns to zero of the driving voltage. The movement was controlled by means of a triode (RCA 5734) the anode of which was mechanically movable. The valve's pin was coupled to the oscillating rod by means of wax colophony. This arrangement permitted observation of the rod movements which appeared on the oscilloscope screen as anode voltage variations. The linearity of the mechano-electrical signal conversion was guaranteed by the small loudspeaker amplitude (µm-range) which was matched by the anode pin's angular deflection of a maximum of 0.5 degrees. In order to achieve a linear movement even at deflection times of a few milliseconds it was not sufficient to feed a corresponding voltage into the system, because the electric signal was deformed by the loudspeaker's oscillation properties. By means of a diode function generator a sawtooth voltage was, therefore, transformed into a piecewise linear voltage of seven segments which was adjusted until the ascending slope of the loudspeaker movement was linear (Fig. 1, $t_R = 2$ ms). The loudspeaker's return-to-zero time was inferior to the rise time by at least the factor 3. At rapid movements ($t_R < 5$ ms, corresponding to hair deflection velocities of $\omega \gtrsim 1$ deg/ms) the return movement was overshooting (cf. Fig. 1 b, $t_R = 2$ ms). Since the hair joined this movement minor disturbing stimuli occurred in the intervals between the stimuli. In the evaluation these disturbing stimuli were neglected.

The loudspeaker was mounted to a Leitz micromanipulator. A thin copper wire was sticked to the end of the aluminium rod. The wire's end was bent and etched thin with nitric acid. Spider and loudspeaker were so arranged that the desired direction of hair deflection was parallel to the direction of movement of the loudspeaker membrane.

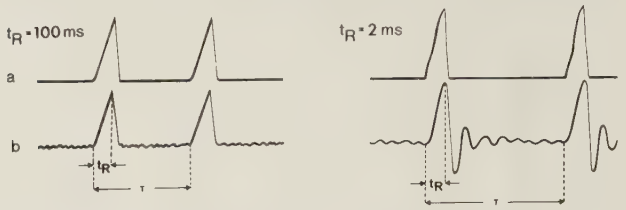

Fig. 1 a and b. Input signal (**a**) and mechanical movement (**b**) of the loudspeaker at varying velocities. t_R stimulus time, τ stimulus period. At rapid deflection there had to be non-linear voltage deformation in order to achieve an approximately linear loudspeaker movement. Further explanation in the text

4. Evaluation

The action potentials were tape-recorded. Since, due to the simple recording method chosen, the signal-to-noise ratio was occasionally disadvantageous (down to an order of magnitude of about 1:1.5) the impulses were formed by means of a comparator.

Data evaluation was mostly carried out by means of a Linc-8 computer (Grüsser team, Physiologisches Institut, FU Berlin). For data acquisition and data rearrangement the latter of which made possible the utilization of programs already existing – special programs were developed. At slow stimuli the computer's small word length (12 bit) required a control of latency on the oscilloscope because additive constants had to be taken into account.

Generally the data printed out by the computer were evaluated manually. The representations of instantaneous frequencies were produced by means of electronic hardware. During the inquiry into adaptation every single deflection was evaluated separately. The rest of the measurements are the mean of several responses.

Results

1. Pulse Train during Single Linear Deflection

Beginning of Pulse Train (7 Receptors). Is a receptor of a trichobothrium stimulated by linear deflection from its resting position action potentials occur at a deflection angle of $\alpha \approx 3$ degrees (Table 2, last column) with medium hair deflection velocity ($10^{-2} \lesssim \omega \lesssim 1$ deg/ms). This deflection angle does not tell anything about the organ's sensitivity with regard to stronger stimulation. For $\omega \approx 1$ deg/ms reaction will occur at deflection angles of 4 to 5 degrees only, for higher stimulus velocities the responses will start at even greater angles. Under these conditions not only the beginning but the entire pulse train will be phase-shifted compared to the stimulus. At $\omega \approx 6$ deg/ms discharges will not start before the ramp stimulus will have passed.

Pulse Rate (7 Receptors). For $10^{-2} \lesssim \omega \lesssim 10^{-1}$ deg/ms the pulse rate shows no monotonous change during a complete deflection (Fig. 2a). With not too rapid deflection ($\omega \lesssim 10^{-1}$ deg/ms) some receptors produce a volley-like discharge pattern, an effect reflected in the plotting of the instantaneous pulse rate by

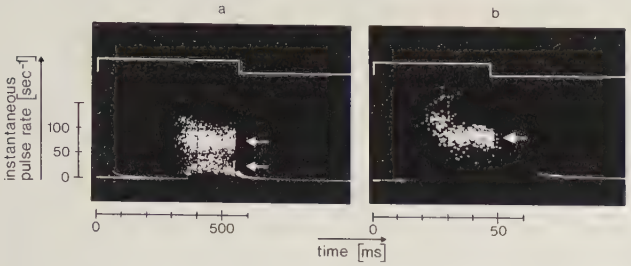

Fig. 2a and b. Instantaneous pulse rate of a receptor at distad deflection. Deflection angle $\alpha = 9.6$ deg, velocities $\omega = 1.7 \cdot 10^{-2}$ deg/ms (**a**) and $\omega = 2.1 \cdot 10^{-1}$ deg/ms (**b**). Arrows indicate the levels with pulse rate accumulations. 40 stimuli, $t_R : \tau = 1:4$. *Tegenaria*, male, 3rd hair from proximal, median row. $l = 203$ µm

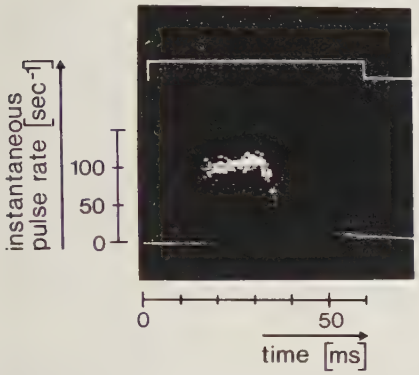

Fig. 3. Cessation of pulse train. Distad deflection, $\alpha = 35.3$ deg, $\omega = 0.64$ deg/ms, 40 stimuli, $t_R : \tau = 1:4$. Pulses cease when the hair appears to have reached the bothrium edge ($\alpha \approx 18$ deg). *Tegenaria*, female, 3rd hair from proximal, median row

Table 1. Correlation between bothrium edge determined by means of sound and cessation of pulse train. Deflection velocities at about 0.5 deg/ms. Average deviation of angle caused by visual measurement ± 1 deg. S.E. of mean of angle inferred from length of pulse train ± 0.5 deg (20 stimuli)

	Bothrium edge at	Pulse train	Deflection
Distad deflection	10 deg	Longer intervals from 11.4 deg on	14 deg
	18 deg	Cessation at 21.2 deg	35 deg
	19 deg	Cessation at 19.2 deg	25 deg
	14 deg	Cessation at 12.9 deg	22 deg
Proximad deflection	11 deg	Continuation till end of stimulus	29 deg
	13 deg	Continuation till end of stimulus	25 deg
	12 deg	Continuation till end of stimulus	42 deg
	11 deg	Continuation till end of stimulus	27 deg

the accumulation of points in the proximity of two discharge rates (Fig. 2a, arrows). Mostly the groups are more distinct at the beginning of a response. Grouping cannot be observed for stimuli of $\omega > 10^{-1}$ deg/ms. In this range the initial pulse rate diminishes in the beginning and then remains on an

Table 2. Stimulus data for adaptation measurement. Last column contains average values of first measurement of both measurement series. Blanks indicate incomplete measurements

Exp. series	Angular velocity ω[deg/ms]	Period of stim. τ[ms] ($t_R : \tau \approx 1:4$)	Period of stim. τ[ms] ($t_R : \tau \approx 1:2$)	1st AP at deflection angle [deg]
a	$5.97 \cdot 10^{0}$	$7.40 \cdot 10^{0}$	—	0
b	$2.39 \cdot 10^{0}$	$1.52 \cdot 10^{1}$	—	8.2
c	$1.06 \cdot 10^{0}$	$3.75 \cdot 10^{1}$	$1.22 \cdot 10^{1}$	5.0
d	$5.80 \cdot 10^{-1}$	$6.10 \cdot 10^{1}$	$3.00 \cdot 10^{1}$	3.1
e	$2.10 \cdot 10^{-1}$	$1.96 \cdot 10^{2}$	$9.80 \cdot 10^{1}$	3.1
f	$1.10 \cdot 10^{-1}$	$3.85 \cdot 10^{2}$	$1.90 \cdot 10^{2}$	3.2
g	$6.00 \cdot 10^{-2}$	$6.10 \cdot 10^{2}$	$3.05 \cdot 10^{2}$	3.1
h	$1.70 \cdot 10^{-2}$	$1.94 \cdot 10^{3}$	$1.00 \cdot 10^{3}$	2.9
i	$1.00 \cdot 10^{-2}$	$3.85 \cdot 10^{3}$	$1.94 \cdot 10^{3}$	2.8

almost even level from $\alpha \approx 5$ degrees till the receptor ceases to respond (Fig. 2b, arrow). Investigations on the properties and biological significance of the volley discharge will be described in another paper (cf. also Wiersma et al., 1970).

End of Pulse Train. When a trichobothrium is deflected by sound observation through a binocular microscope indicates at what amplitude the bothrium's edge appears to be reached. It is here that the otherwise evenly blurred picture of the moved hair looks different. Recordings reveal that the pulse train at distad hair deflection is distorted at about the same deflection angle (Fig. 3), whereas receptors stimulated by proximad deflection show no disturbance effect at all (Table 1). With deflection by sawtooth stimuli within the bothrium the spikes at $\omega \lesssim 1$ deg/ms cease a few milliseconds after the end of stimulation (cf. Fig. 2b).

2. *Adaptation Caused by Repeated Stimulation*

Preliminary experiments showed that repeated hair deflection results in receptor adaptation when the interval between two stimuli is of the same order of magnitude as the deflection time. Since longer experimental series had to be carried out under equivalent conditions a stationary response could practically not be achieved.

a) Adaptation at Different Hair Deflection Velocities

Stimulation Program. The following program for repeated stimulation was performed. A linear deflection with a definite angular velocity (e.g. $\omega = 10^{-2}$ deg/ms) was followed by a rapid return into the resting position and an interval of definite length (cf. Fig. 1). Every single response was evaluated separately. Experimental series of this kind were carried out with intervals of varying lengths. The ratios of stimulation times t_R and stimulation periods τ were about 1:4, 1:3, 1:2, 1:1.5 and 1:1.25 (Table 2).

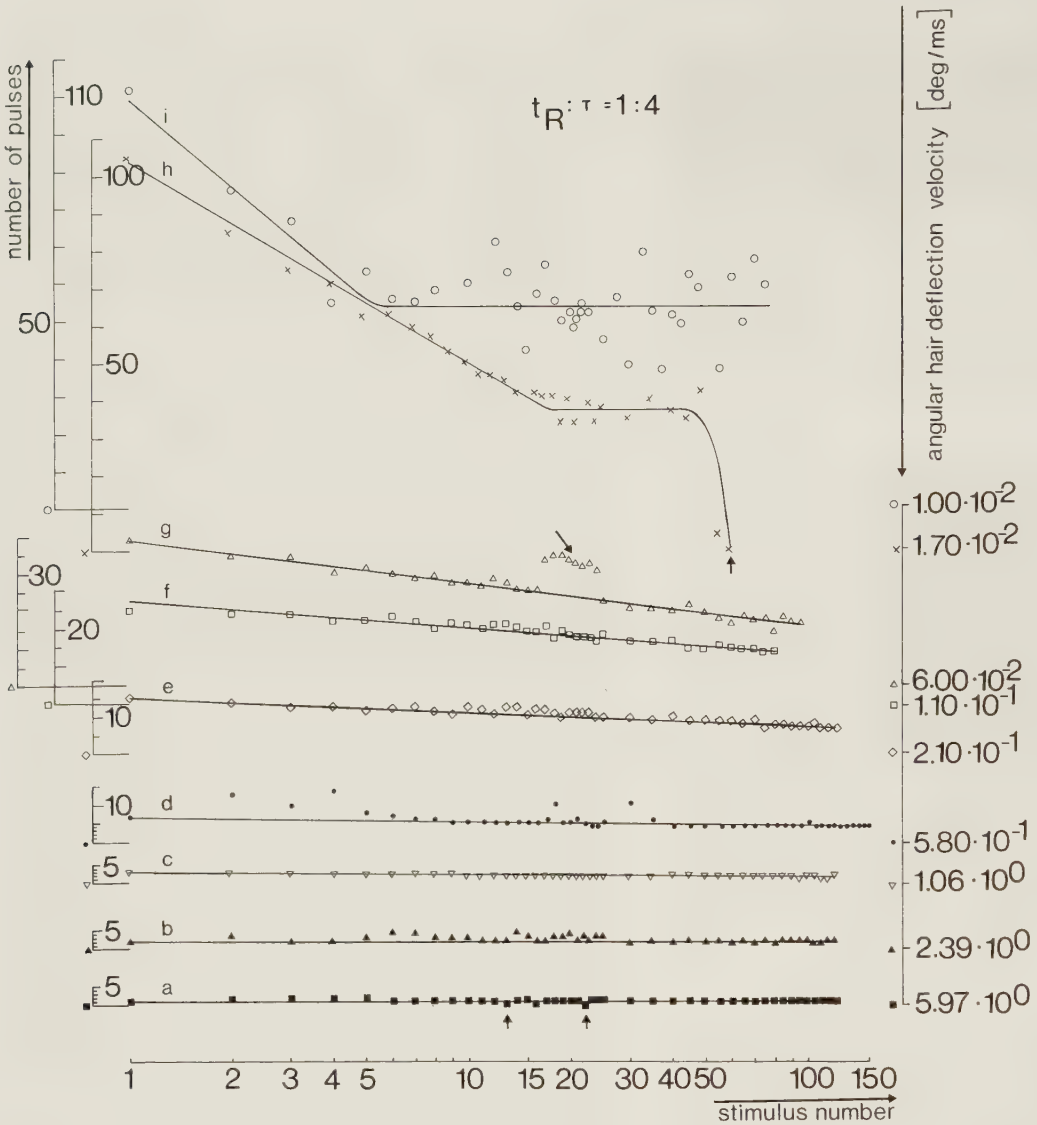

Fig. 4. Number of pulses as function of stimulus number at repeated distad deflection of trichobothrium. Right pedipalpus, median row, 3rd hair from proximal, $l = 203$ µm. t_R stimulus time, τ stimulus period, ω angular velocity of hair. Each curve with its own ordinate scale (left), corresponding zero point is marked by symbol. On a level with zero line (right) indication of hair deflection velocity. Co-ordinate systems shifted against each other in the direction of y-axis according to the deflection velocity in logarithmic scale. x-scale identical for all curves. Vertical arrows indicate non-occurrence of pulses at a stimulus. Further explanations in the text

The experiments started with an angular velocity of about 10^{-2} deg/ms corresponding to a deflection of 10 degrees at a stimulation time of $t_R = 1$ s. Deflection velocities were gradually increased. Since the experimental animals often did not remain motionless and since an experimental series took more than an hour the stimulation program could not always be entirely fulfilled.

From a total of 8 receptors 2 were investigated by covering a wide range of angular hair deflection velocities ($10^{-2} \lesssim \omega \lesssim 6$ deg/ms). The following is an exemplary description of one of them.

For adaptation measurements the number of pulses per individual stimulus and latency normalized to the stimulus time were used. Supposed that the spike intervals do not change on the average then the number of pulses is a measure for the time the generator potential of which is above threshold. The condition of intervals being equal is fulfilled with sufficient precision for all $\omega > 1.7 \cdot 10^{-2}$ deg/ms (cf. discussion of errors, below). The adaptation of a receptor to repeated hair deflection is presented in Table 4 and Figures 4 to 7. The hair was deflected distally with an angle of 9.55 degrees. The adaptation of the opposite receptor reacting to proximad deflection was measured under equal conditions; the results being similar.

In Figure 4 the points of every measurement series

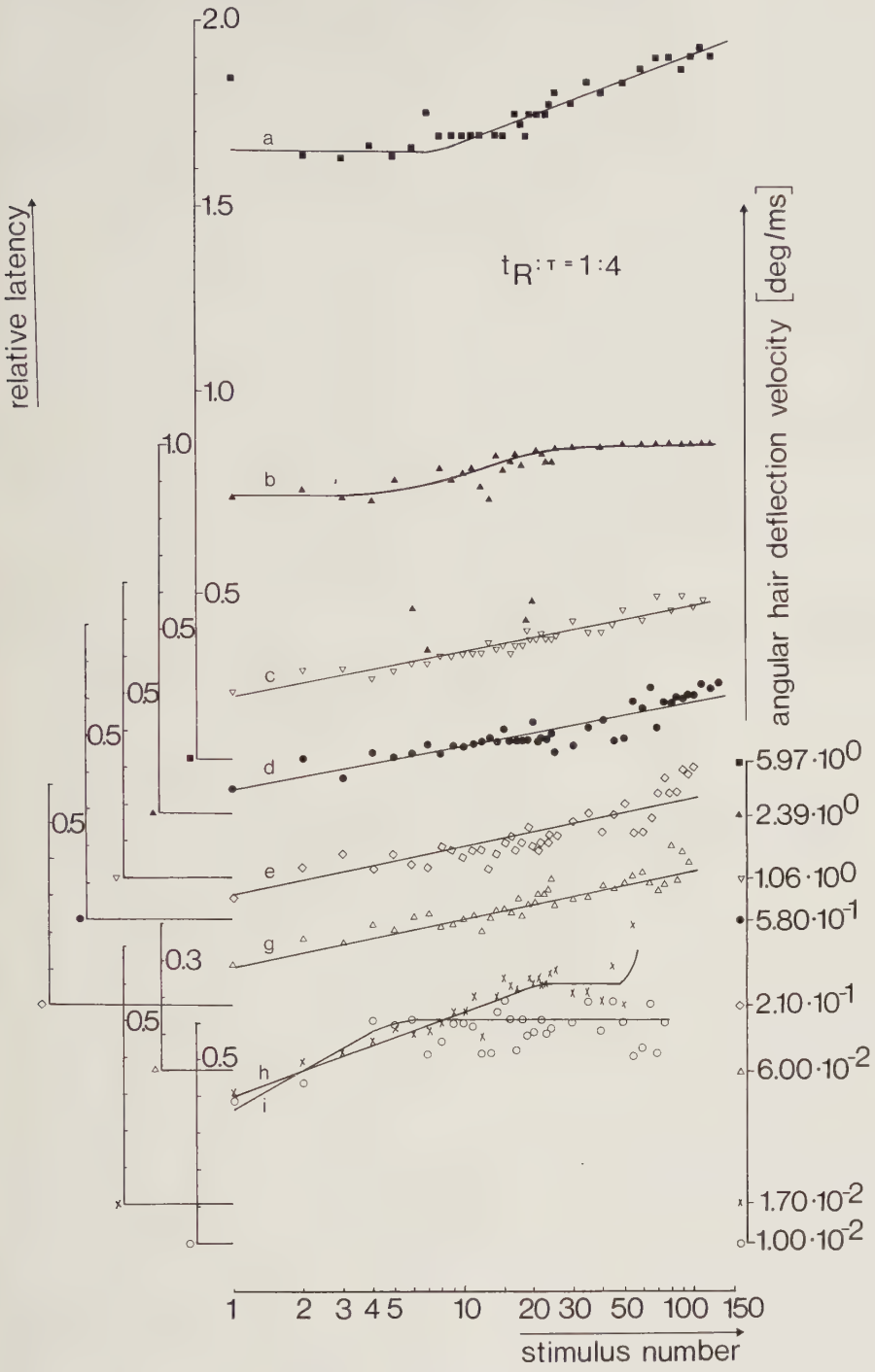

Fig. 5. Latency of receptor (cf. Fig. 4) at repeated stimulation, normalized to stimulus time. Curve f, approximately congruent with curve g, is rendered. Further explanations in the text

could entirely (curves a to g) or at least partly (curves h and i) be fitted to straight lines. The number of pulses per stimulus is small at highest deflection velocities ($6 \lesssim \omega \lesssim 1$ deg/ms, curves a to c) and remains almost constant from the first to the 130th stimulus. Adaptation increases with diminishing deflection velocities. At $\omega = 1.7 \cdot 10^{-2}$ deg/ms (curve h) the first stimulus elicits 105 discharges, whereas no reaction whatever occurs at the 60th stimulus (arrow). At lowest deflection velocities (curves h and i) an initially strong adaptation is followed by a discharge rate which is constant on the average. The discharge rate at $\omega = 10^{-2}$ deg/ms (curve i) shows great variation. It appears that the mean discharge does not vary

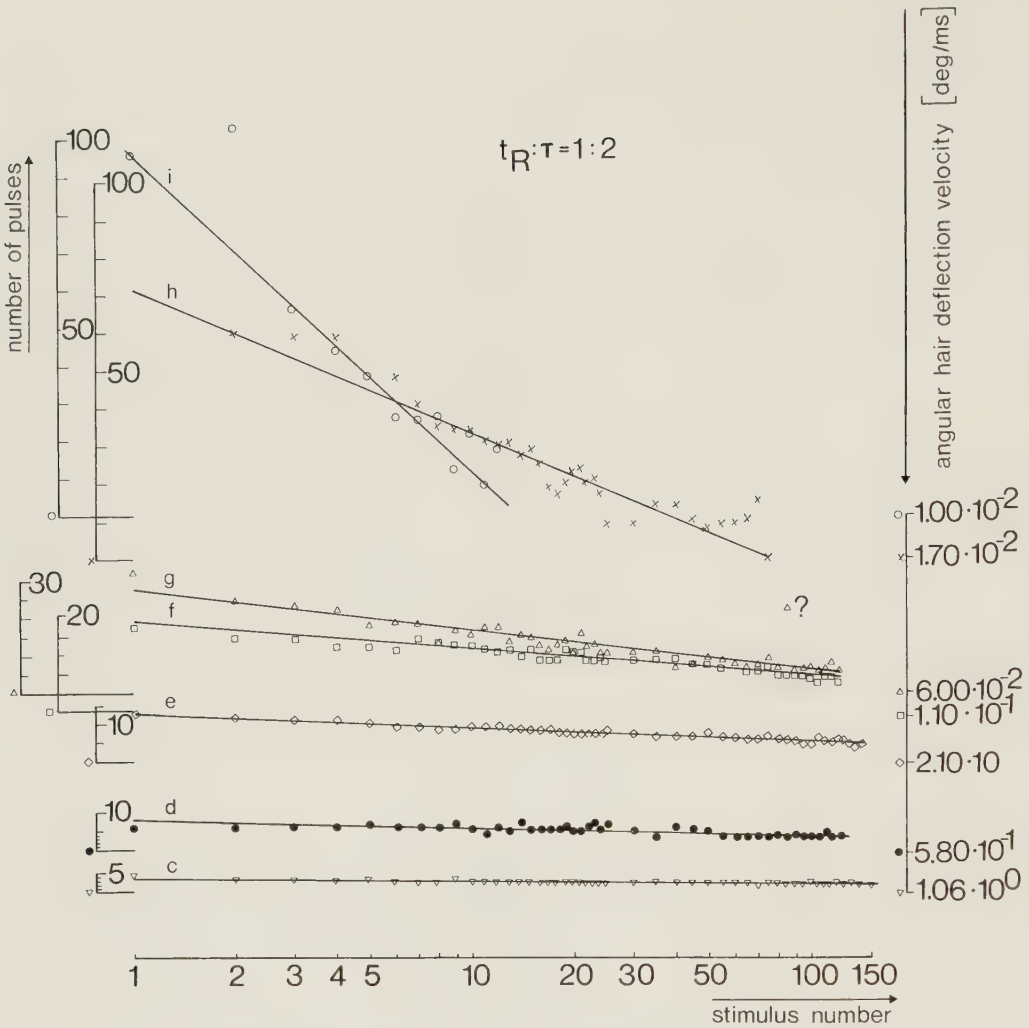

Fig. 6. Number of pulses as function of stimulus number (same receptor as in Figs. 4 and 5) at stimulation with duty cycle changed. The highest deflection velocity $\omega = 1 \cdot 10^{-2}$ deg/ms, therefore non-existence of curves corresponding to a and b in Figure 5. Further explanations in the text

because an adaptational process (during stimulation) and a process of recovery (during pauses) are counterbalancing each other.

Receptor latencies as a function of hair deflection velocities are plotted in Figure 5. Compared to Figure 4 the co-ordinate systems are shifted in reverse order (cf. right ordinate scales of both figures). The latencies t_L are normalized to stimulus duration t_R (left ordinate scales)[1].

The curves c to g are complementary to the corresponding curves in Figure 4: the increase in relative latency goes along with a decrease in number of pulses. The greater steepness of the first piece of curve h compared to that of curve i demonstrates that during the course of the stimulation series the inter-spike intervals increase exceedingly (84% increase from 1st to 20th stimulus). This result is not typical. The second receptor investigated has bends in the latency curves similar to those in Figure 5. These bends, however, occur more frequently. The first piece of the curve is generally of minor steepness. Thus, latency increase during repeated stimulation is variable.

Figures 6 and 7 show adaptation in the same receptor with intervals between deflections shortened ($t_R:\tau \approx 1:2$). The number of pulses (Fig. 6) can be fitted to a straight line up to the lowest deflection velocities ($\omega = 1.00 \cdot 10^{-2}$ deg/ms, curve i). The negative increase of the curves sinks progressively from low to high velocities. This corresponds to a steady decrease in latency (Fig. 7).

The adaptation curves depend logarithmically on

[1] This normalization means: for $t_L \to t_R$ the value $\hat{t}_L \to 1$, i.e. latency→stimulus duration which is tantamount to complete adaptation for not too high velocities

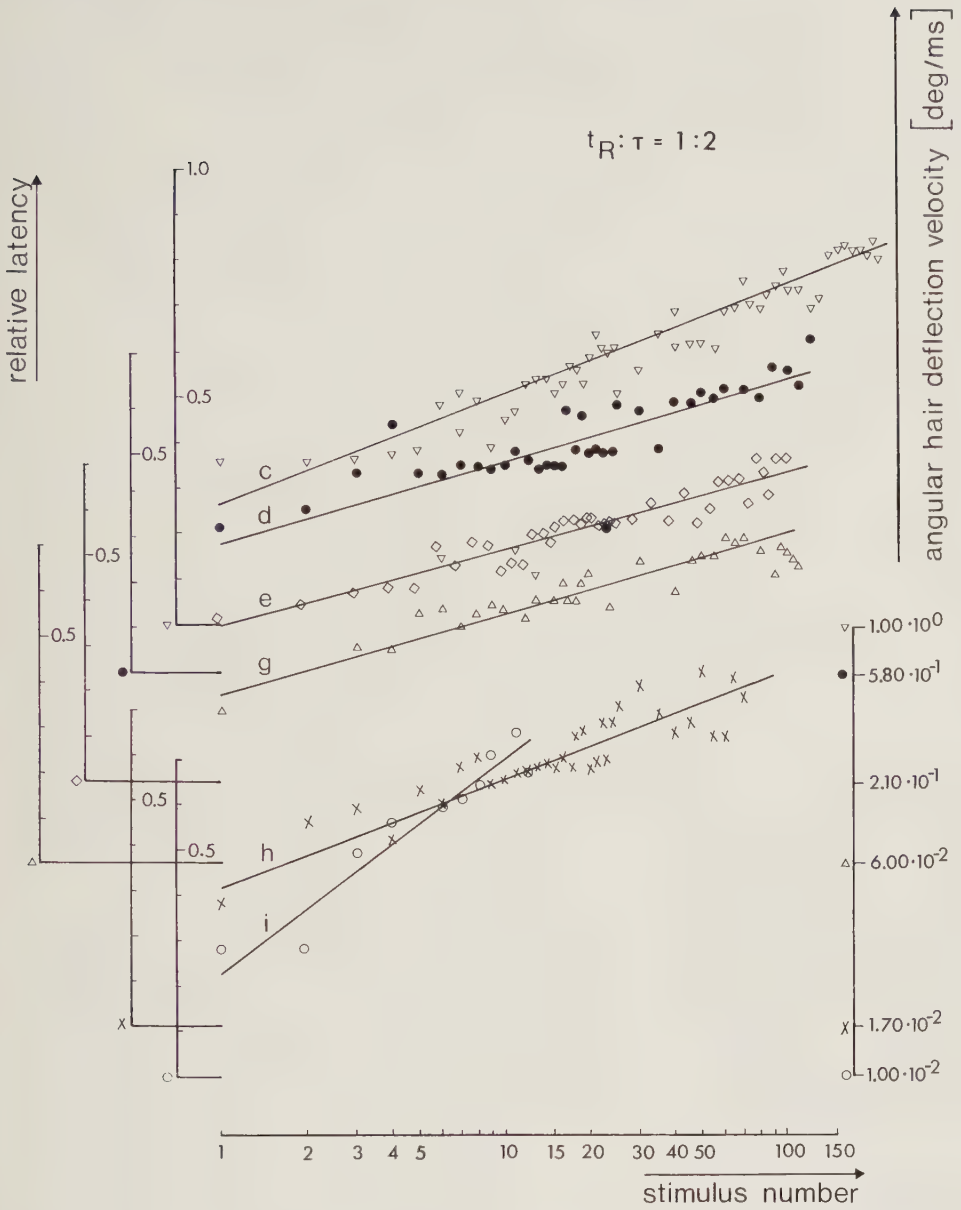

Fig. 7. Normalized latency of receptor (cf. Figs. 4 to 6) with $t_R:\tau=1:2$. Complementary to Figure 6

the stimulus number. For the number of pulses the following equation holds:

$$n\left(\omega,\frac{t_R}{\tau}\right)=n_0\ (\omega)-k\left(\omega,\frac{t_R}{\tau}\right)\log m.^2 \qquad (1)$$

n_0 is the number of pulses of the first response, m the stimulus number and k, in accordance with the scales used, the steepness of the curve. The initial value n_0 and the parameter k are functions both of the deflection velocity and of the duty cycle. The numerical values for one receptor are listed in Table 3 (columns 3 to 5). With hair deflection velocities decreased, both parameters rise accordingly.

Adaptation was investigated on two receptors of the same trichobothrium. Comparison of the results did not reveal differences that were to be ascribed to the receptors' different position at the organ's basis. Because of lack of further examples, however, different adaptational properties of complementary sense cells cannot be excluded.

Similar to the curves for the numbers of pulses the latency curves are logarithmic functions of the stimulus numbers as well when they are not parallel

[2] The left side of the equation is an integer. Fractions on the right side must, therefore, always be rounded to meet the requirements of the equation

Table 3. Initial values n_0 (ω) of numbers of pulses and of relative latency $\hat{t}_{L_0}$ and coefficients $k(\omega)$ and κ (ω) of the corresponding logarithmic functions of the receptor, taken from Figures 4 to 7. Except for the first two lines, n_0 and $\hat{t}_{L_0}$ are the average of the values of both series of measurement. The asterisked values refer to the first descending pieces of the curves h and i in Figure 4 and to the ascending pieces of the corresponding curves in Figure 5, respectively. Further explanations in the text

Exp. series	ω deg/ms	n_0 (ω)	k (ω)		$\hat{t}_{L_0}$ (ω)	κ (ω)	
			$t_R:\tau=1:4$	$t_R:\tau=1:2$		$t_R:\tau=1:4$	$t_R:\tau=1:2$
a	$5.97\cdot10^{0}$	1	$3\cdot10^{-3}$	–	1.65	$4\cdot10^{-1}$	–
b	$2.39\cdot10^{0}$	2	$6\cdot10^{-3}$	–	0.86	(irregular curve)	–
c	$1.06\cdot10^{0}$	3	$9\cdot10^{-3}$	$1\cdot10^{-2}$	0.39	$2\cdot10^{-1}$	$4\cdot10^{-1}$
d	$5.80\cdot10^{-1}$	7	$1\cdot10^{-2}$	$2\cdot10^{-2}$	0.32	$2\cdot10^{-1}$	$3\cdot10^{-1}$
e	$2.10\cdot10^{-1}$	14	$4\cdot10^{-2}$	$4\cdot10^{-2}$	0.32	$2\cdot10^{-1}$	$3\cdot10^{-1}$
f	$1.10\cdot10^{-1}$	24	$8\cdot10^{-2}$	$8\cdot10^{-2}$	0.33	$2\cdot10^{-1}$	$3\cdot10^{-1}$
g	$6.00\cdot10^{-2}$	34	$1\cdot10^{-1}$	$1\cdot10^{-1}$	0.32	$2\cdot10^{-1}$	$3\cdot10^{-1}$
h	$1.70\cdot10^{-2}$	81	$6\cdot10^{-1*}$	$4\cdot10^{-1}$	0.30	$5\cdot10^{-1}$	$4\cdot10^{-1}$
i	$1.00\cdot10^{-2}$	105	$8\cdot10^{-1*}$	$9\cdot10^{-1}$	0.29	$4\cdot10^{-1}$	$7.5\cdot10^{-1}$

to the x-axis (cf. Figs. 5 and 7). Analogously to equation (1) the following equation holds:

$$\hat{t}_L\left(\omega, \frac{t_R}{\tau}\right) = \hat{t}_{L_0}(\omega) + \kappa\left(\omega, \frac{t_R}{\tau}\right) \log m. \quad [2] \qquad (2)$$

In this equation t_{L_0} is the initial value of the normalized latency time. The numerical values of t_{L_0} and κ are listed in Table 3 (columns 6 to 8). These values are constant in the range $6\cdot10^{-1} \lesssim \omega \lesssim 6\cdot10^{-2}$ deg/ms.

The preceding passages described quantitatively the adaptation of one receptor of a trichobothrium with view to relative latency and number of action potentials per stimulus. The opposite receptor showed corresponding adaptation. The evaluations of measurements on other receptors indicate similar adaptation properties.

The evaluation of measurements with view to the mean pulse rate revealed that the latter is also subject to adaptational change (Table 4). The average pulse rate for the curves h and i, i.e. for $\omega \lesssim 1.7\cdot10^{-2}$ deg/ms is very high. This means that repeated stimulation alters the information about the deflection velocity, provided that the information is encoded in pulse rate.

Table 4. Mean pulse rate at repeated stimulation (cf. Fig. 6). In series c there were 1 to 2 pulses per stimulus only

Curve	Stimulus number	Mean pulse rate [sec^{-1}]	Fractional decrease in pulse rate
d	1	561	9.6
	120	508	
e	1	455	3.7
	100	438	
f	1	466	14.2
	80	400	
g	1	340	15.9
	90	286	
h	1	278	43.9
	20	157	
i	1	196	29.0
	5	139	

b) Adaptation at Stationary Deflection prior to Stimulus

In Figure 8a to c deflection was varied at the beginning of the stimulus. For 4 min the trichobothrium was kept in its resting position (curve a) or in a position corresponding to a deflection angle of 1.91 degrees (curve b) or a deflection angle of 3.82 degrees (curve c). After this conditioning stimulus the trichobothrium was deflected with constant velocity. The initial values n_0 of the medium initial amplitude (curve b) are inferior to those of the greatest (curve c), a result differing from that of a second receptor investigated. The steepness of the descending slope, however, increases from (a) to (c), a fact which corresponds to measurements of the other receptor inquired into. Thus, at repeated stimulation, a deflection with an initial angle greater than zero results in a more rapid decline of the number of pulses. Similar results were achieved by Hoffmann (1967) in *Euscorpius*.

[2] See footnote p. 77

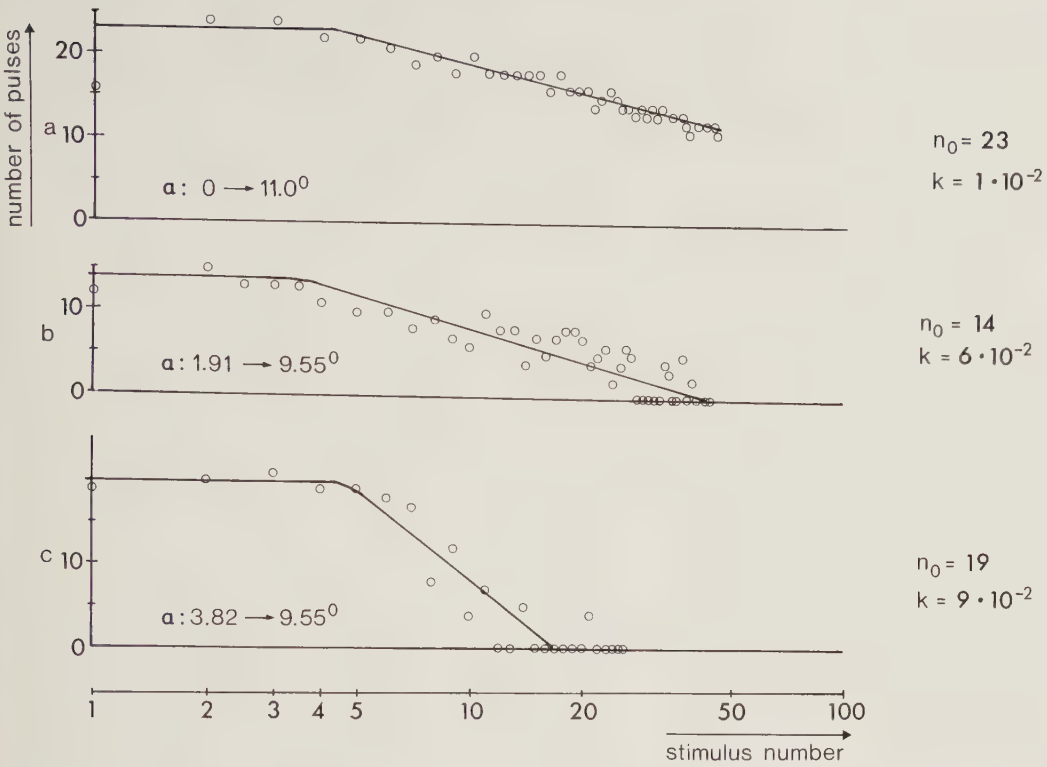

Fig. 8. Course of adaptation brought about by repeated stimulation after static conditioning stimulus. Duration of static deflection 4 min. α conditioning deflection angle, $\omega = 1.15 \cdot 10^{-1}$ deg/ms, $t_R : \tau = 1 : 3.9$. *Tegenaria*, male, nymph, left pedipalpus, 3rd hair from proximal, median row, $l = 307$ µm

These and all the other measurement series described could lead to reproducible results only because the experimental animals were tightly pinned to their support. When they were given the slightest freedom of movement they at first kept quiet for a while but then started moving and, immediately afterwards, responded to a stimulation identical with the preceding one with a substantially higher rate of discharge.

Discussion of Errors. Typical of the experiments described is that all experimental measurement errors are negligible compared with the biological variations in the receptor response. The values for the input variables given in Table 2 contain maximal errors of ±2%. The measuring error of time measured by stop watch (cf. last column) amounted to 3% at a maximum. In data acquisition, occasionally, an impulse was not counted. This error, however, is eliminated by the fitting curves.

Measurement deviations of stochastical as well as of systematical nature brought about by physiological phenomena outweighed the above mentioned sources of error by far. Random variations due, for instance, to receptor potential noise are made up by the fitting curves, whereas systematical variations are generally concealed. Systematical deviation from the fitting curve occurs in all likelihood between stimulus number 17 and stimulus number 25 in measurement series g (oblique arrow) in Figure 4. The seemingly greater dispersion of the latencies compared with the number of pulses is generally due to normalization (larger $\hat{t}_L$ – scale). The values of the constants k and κ (cf. equations (1) and (2)) rendered in Table 3 contain a mean deviation of about ±30% due to logarithmic extrapolation. The fitting curves are, moreover, drawn according to visual estimate, which, however, is legitimate with view to the receptor's long-time variations observed because physiological variations are certainly of greater weight.

In so far as curves h and i (Figs. 4 and 6) are interpreted as presentations for the time during which the generator potential is above threshold (cf. Results, Sect. 2(a)) another systematical error must be considered. An estimation of the correction factors for the curve rise results in values between 1.4 and 1.9 (for the other curves the values are between 1.04 and 1.2).

The values of the parameter $t_R : \tau$ given in Figures 4 to 7 do not exactly amount to $^1/_4$ or $^1/_2$ (the precise values can be gathered from Table 2 because of $\alpha = 9.55$ deg). The resulting standard error of mean of ±10% enters into the error of k and κ. This, however, does not affect the conclusions drawn from the experiments.

3. Pulse Rate as Function of Deflection Velocity

7 receptors were analyzed with view to the dependency of latency time and average pulse rate on the hair's deflection velocity. Figure 9 renders the results of 3 physiologically detectable receptors of a single trichobothrium. Responses of 10 to 20 successive stimuli were averaged. While the latency curves in semi-logarithmic plotting are bent the curves of the average pulse rates are approximately linear. Thus the pulse

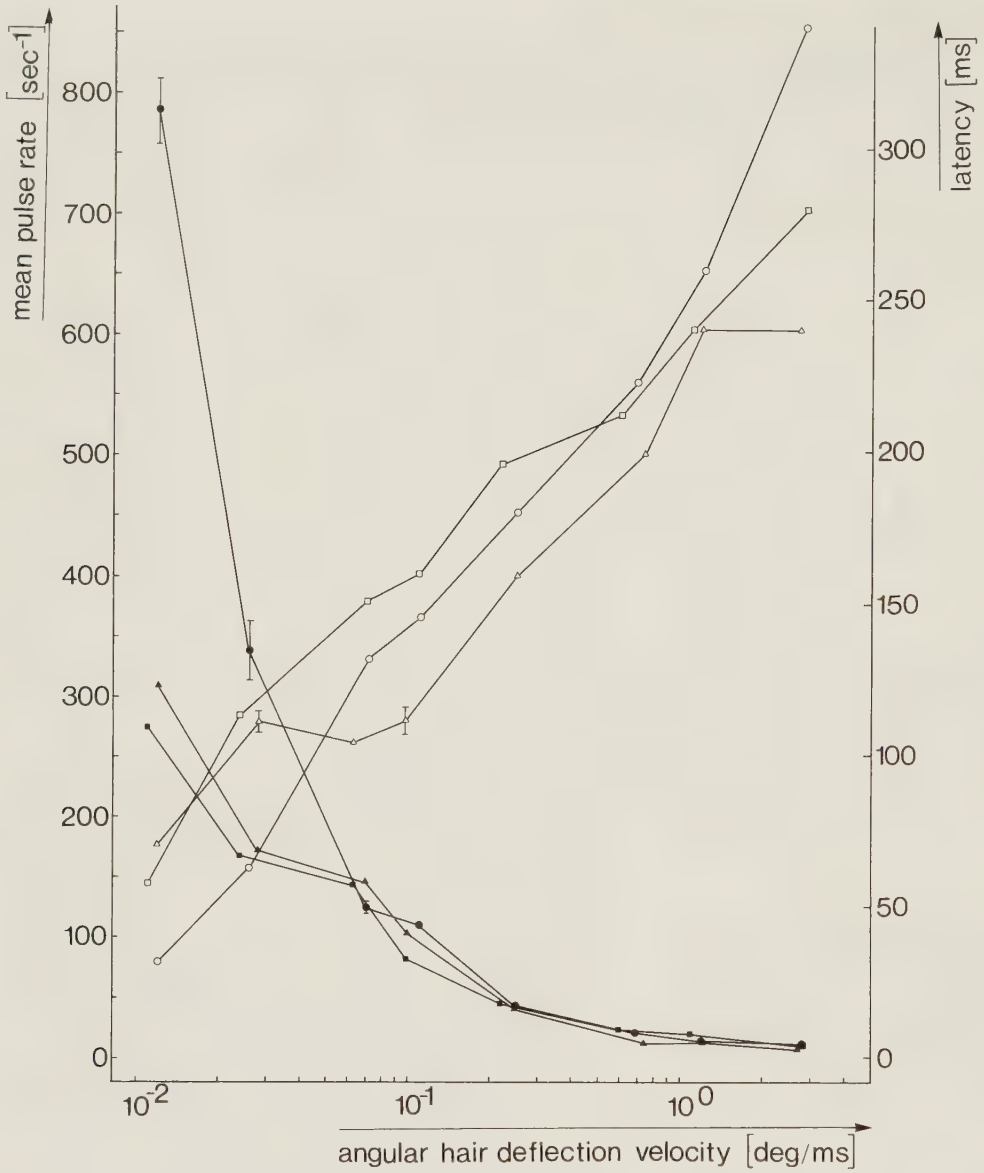

Fig. 9. Latencies (filled symbols) and mean pulse rates (non-filled symbols) of three receptors of same trichobothrium. Distad deflection (curves a, $\alpha = 11.0$ deg), proximad deflection (curves b, $\alpha = 11.0$ deg) and distad approximately transversal deflection (curves c, $\alpha = 9.9$ deg), 10 to 20 stimuli ($t_R : \tau = 1:4$). Error: S.E. of mean and range of variation for pulse rate curves at $\omega \gtrsim 10$ deg/ms. *Tegenaria*, male, nymph, left pedipalpus, 3rd hair from proximal, median row, $1 = 307\ \mu m$

rate is a logarithmic function of ω. This result was confirmed by measurements of two other cells.

It is true that taking the average of several successive responses to stimuli is a means of diminishing accidental errors, but it results in systematical deviations on account of the adaptation occurring: as a rule, latencies are longer and pulse rates smaller than at a single deflection, due to gaps in the pulse train occurring during adaptation. The characteristics of two other receptors were based on data received from the first response only. The result is quantitatively similar to that rendered in Figure 9.

The receptor's threshold sensitivity with respect to the deflection angle is a function of stimulus intensity, too: at high deflection velocities a deflection angle of $\alpha \lesssim 1$ degree is sufficient for pulse release (Görner and Andrews, 1969); at medium deflection velocity the threshold angle is $\alpha \approx 3$ degrees (Table 2).

4. Directional Sensitivity

6 trichobothria were deflected under various azimuthal angles in order to determine their entire azimuthal range of response. Deflection velocities and amplitudes were kept constant. The mean pulse rate of

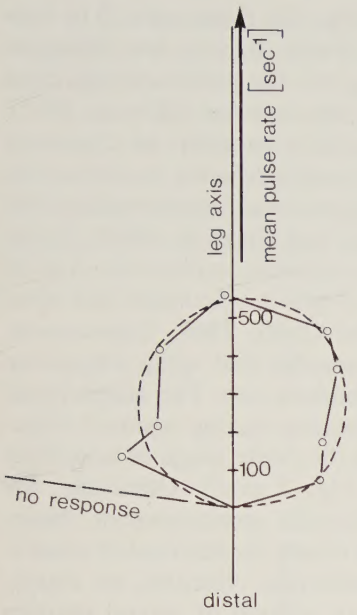

Fig. 10. Directional sensitivity of a trichobothrium receptor at linear hair deflection. $\omega = 1.2 \cdot 10^{-1}$ deg/ms, $\alpha = 12.1$ deg. Error: S.E. of mean of pulse rate smaller than round symbols, error of azimuthal angle ± 4 deg left and ± 1 deg right of leg axis. Fitted cosine curve dashed. Dashed straight line left symbolizes direction of an actual deflection, for technical reasons corresponding direction right not precisely determined. *Tegenaria*, male, 2nd hair from proximal, median row, $l = 283$ µm

a receptor is plotted as a polar diagram in Figure 10, the azimuthal angle being the independent variable. The measurement points represent as a rule 20 successive deflections ($t_R : \tau = 1 : 8$). The curves can be fitted by a cosine function. Curve fitting was performed in the *xy*-diagram. Measurements of other receptors confirm the cosine-similar dependency of the azimuthal response.

Discussion

1. Pulse Train at Uniformly Deflected Hair

When a trichobothrium receptor is stimulated by deflection of the hair with a uniform angular velocity ($10^{-2} \lesssim \omega \lesssim 1$ deg/ms) it responds by release of pulses of medium rates which are preserved in the mean, except perhaps for the beginning of the response. The pulse train elicited may, however, be interrupted by pauses. With the system still unadapted, discharges will start at an angle of hair deflection of 2 to 3 degrees (the threshold angle of hair deflection of about 1 degree mentioned by Görner and Andrews (1969) was measured at higher deflection velocities). In the organs of scorpions resembling those of spiders a comparable deflection angle is required for eliciting action potentials (Hoffmann, 1967). It might be supposed that this is brought about by mechanical filtering in the stimulus transducing apparatus (cf. Mendelson and Loewenstein, 1964; Loewenstein, 1971; Gaffal, 1976). Since stimuli, however, are directly transduced from hair to dendrite (cf. Christian, 1971, 1972) this does not seem probable. The reasons for this must, therefore, be looked for in the receptor itself.

Responsible for the mechano-electric transduction is, in all likelihood, the compression of the dendrites' tubular body (cf. Görner, 1965; Christian, 1971, 1972; Barth, 1972; Gaffal and Hansen, 1972; Thurm et al., 1974; Barth and Pickelmann, 1975; Gaffal, 1976). In the trichobothrium compression of the tubular body is determined by the angle of hair deflection. This angle is slightly inferior to that measured here because from the beginning of the compression of the tubular body till the release of the first action potential a certain time goes by. This interval depends among other factors on the steepness of the generator potential increase and thus on ω. The delay between compression of tubular body and beginning of change of the generator potential will be 0.1 ms only (Thurm, 1964). Latency is thus essentially composed of three phases, (1) interval between beginning of stimulus and compression of tubular body, (2) period of increase of generator potential till occurrence of excessive threshold and (3) period of formation of first action potential.

With rapid deflection ($\omega \gtrsim 1$ deg/ms) the angle of the first spike released exceeds 2 to 3 degrees (cf. Fig. 5, curve b, first stimulus). At $\omega \approx 6$ deg/ms pulses occur after the hair's return to its resting position only (Fig. 5, curve a, relative latency 1.64). With such deflection velocities the most important latency component is the time of delay between the compression of the tubular body and the occurrence of the first action potential. Counting from the moment at which the hair is deflected by an angle of 3 degrees it amounts to 1.8 ± 0.4 ms (average value of curves a, b, c in Fig. 5). Equal computation for another receptor leads to 1.1 ± 0.3 ms. Thus, nothing definite can be said so far about the receptor's sensitivity to deflection angles at high deflection velocities (cf. Görner and Andrews, 1969).

As far as trichobothria are concerned a constant adequate stimulus, i.e., a uniform hair deflection velocity can only occur between the resting position ($\alpha = 0$) and the contact with the bothrium edge. According to determination by air sound the bothrium edge is reached at $\alpha = 10$ to 19 degrees; according to direct observation through binocular microscope the contact with bothrium edge occurs at 13 to 23 degrees (Görner, 1965). With hair deflection beyond bothrium

edge the result differs in accordance with stimulus direction: at distad deflection pulses cease when the hair reaches the point which, according to the dynamic deflection (air sound), corresponds to the edge of the bothrium, whereas the opposite receptor continues to discharge even after having reached this point (cf. Table 1). The polar behaviour of the receptor response could be explained by the asymmetrical structure of the hair basis (Görner, 1965; Christian, 1971, 1972). Below the bothrium membrane the hair is of furrow-like shape so that the connection with the adjacing helmet could possibly react to hair deflection parallel to the longitudinal leg axis in mechanically different ways because the elastic properties of the hair basis vary according to the direction of hair deflection. A bothrium edge asymmetry might also be of importance: in the symmetrical club-shaped sensilla on the cerci of *Gryllus* for instance there is no inhibition observable at exceeding hair deflection (Bischof, personal communication). Thus, the different responses of the trichobothria receptors to exceeding deflection may probably be explained by mechanical causes. At exceeding proximad deflection the hair basis possibly moves in the same way as it does at trapezoidal hair deflection within the bothrium because, in both cases, receptor activity gradually dies away. Mechanical inhibition at exceeding distad deflection could well correspond to inhibition resulting from return to resting position of a saw-tooth stimulus.

2. *Adaptation*

Adaptation can either be measured as change in receptor response to uniform stimulus succeeding to a static conditioning stimulus or at repeated stimulation (cf. Loewenstein, 1971). Experiments were carried out for both.

Hoffmann (1967) deduced from his recordings on trichobothria in *Euscorpius* that, at repeated stimulation, two different adaptational processes occur, the first reacting to static and the second to dynamic conditioning stimuli. The present accounts show that, in spiders, a static stimulus has the same effect as dynamic conditioning stimuli.

During a single hair deflection with constant angular velocity pulses are released after a period of latency, which has already been discussed. In the range of medium stimuli ($10^{-2} < \omega < 1$ deg/ms) about half of the receptors inquired into respond with a constant mean rate of discharge as it was already described by Görner (1965). Prior to a decrease in pulse rate down to a constant level the remaining receptors discharge more frequently at the beginning of the reaction. Generally, this decay takes 3 to 4 ms only (in Fig. 2b: 8 to 10 ms). At very low deflection velocities ($\omega < 10^{-2}$ deg/ms) the pulses already cease before termination of the stimulus (Görner, 1965).

Investigations on stretch receptors in Crustacea revealed that here the essential factor in adaptation resides in the trigger region of action potentials (Nakajima, 1964; Nakajima and Onodera, 1969a, b). In the Pacini receptor accommodation plays also a great part in the adaptation of cells (Loewenstein and Mendelson, 1965; Sato and Ozeki, 1966; Loewenstein, 1971). It seems to be possible that spike adaptation can be found in trichobothria, too. The adaptational behaviour in receptor response during repeated stimulation was measured in the entire range of sensitivity of two receptors (cf. Figs. 4 to 7). Obviously, the plasticity of the mechanical structures can immediately be excluded as a reason for this kind of adaptation. For, at lowest deflection velocities, an experimental series covered an interval of several minutes without leading to any differences in the adaptation characteristic when the latter is compared to that resulting from high deflection velocities.

Except for extremely slow stimuli ($\omega < 10^{-1}$ deg/ms) the mean pulse rate varies about 10% only even after more than 100 stimuli. The latency normalized to the stimulus time and the number of pulses per single stimulus were, therefore, used as a measure for adaptation. Successive uniform deflections were evaluated separately. The scaling of the abscissa axis (Figs. 4–7) implies already the assumption that the natural independent variable of adaptation is not the absolute time, but the time measured in units of the stimulus period (i.e., the stimulus number). For medium deflection velocities ($2 \cdot 10^{-1} \lesssim \omega \lesssim 1$ deg/ms) the curves actually follow the same formalism as they are all nearly parallel straight lines in semilogarithmic plotting.

For high deflection velocities ($\omega \gtrsim 2 \cdot 10^{0}$ deg/ms) the latency curves may consist of two pieces with different steepness (cf. Fig. 5, curve b). Since there is experimental evidence for efferent innervation of the trichobothria in scorpions (Ignatjev et al., 1976) it may be assumed that in the present case, too, some efferently induced reduction in sensitivity might be the case.

It seems possible to deduce changes in pulse response during movements of the spider from the same reason as well. Eyzaguirre and Kuffler (1955) noticed for the stretch receptor in Crustacea stronger responses at moments in which the organism's general activity was heightened. Such a heightening of activity certainly occurs during the spider's efforts to get free.

A second way of accounting for the long-term change in the receptor's sensitivity could possibly con-

sist in the existence of humoral control as it was suggested for epidermal receptors in insects (Küppers and Thurm, 1974).

A third mechanism which could be responsible for long-term adaptation is the possible oxygen starvation of an ion pump caused by a blocking in the lymph circulation. The strong dependency of the receptor potential on oxygen supply is, obviously, the norm (Thurm, 1965, 1974) at any rate. This mechanism would help to explain both the heightening of activity during efforts to get free and the described change in adaptation intensity.

The adaptational intensity of trichobothrium receptors is determined by the value of the duty cycle: smaller duty cycles are responsible for smaller decay constants, i.e., for slower adaptation. Adaptational effects are also brought about by stationary deflection prior to the stimulus (Fig. 8). – At low deflection velocities ($\omega \lesssim 2 \cdot 10^{-1}$ deg/ms), too, the receptor adapts more rapidly. At a high duty cycle ($t_R : \tau = 1:4$) it continues to discharge stationary on the average (even if with considerable variation). Eventually the receptor abruptly suspends activity. – At highest deflection velocities ($\omega \gtrsim 1$ deg/ms) which, for technical reasons, were only brought about for $t_R : \tau = 1:4$ a nearly constant number of discharges was linked with at first constant and afterwards increasing latencies.

The ascending pieces of the curves of latency and the descending pieces of those for the number of pulses are logarithmically dependent on time (equations (1) and (2)) since the stimulus number (m) is at constant periods of stimulation a measure for the time (t). For $\omega \lesssim 10^{-1}$ deg/ms the number of pulses can be used as a measure for the duration (y) of the generator potential's being above threshold without having to reckon with an error exceeding about 10%. When in Equation (1) m is replaced by t and n by y differentiation for y leads to a differential equation of the following form:

$$\dot{y} + K\left(\omega, \frac{t_R}{\tau}\right) t^{-1} = 0, \tag{3}$$

the parameter K not being a function of t in the above described domain. For the latency time an analogous relation is arrived at if y is substituted for $\hat{t}_L$ in Equation (2).

Equation (3) formally describes the temporal changes in latency and length of pulse train of the receptor at repeated stimulation.

3. Dependency of Receptor Response on Hair Deflection Velocity

The logarithmic dependence of the pulse rate on the deflection velocity of the hair covers the entire range of measurement (Fig. 9). The range of the receptor cell's sensitivity is therefore comparatively wide (cf. Grundfest, 1975). Although the absolute latencies are monotonously decreasing with ω (Fig. 9), their values related to stimulus time are so increasing in the range superior to $\omega \approx 1$ deg/ms that spikes occur after termination of the stimulus only (Figs. 5 and 7). Here, the organ appears to have reached the limits of its physiological performance. While rapid transients in unidirectional air flow are still perceived this is not the case with periodical air movements: at a duty cycle 1:2 the value $\omega = 1$ deg/ms corresponds to a fundamental oscillation of 1 kHz, a frequency at which the hair hardly displays deflection at all (preceding paper).

The other limit of the range of biological use of the organ might be found at a hair deflection velocity of $\omega \approx 10^{-2}$ deg/ms since the pulse train already ceases at velocity values inferior to this one before the bothrium edge is reached. The electrophysiological measurements are in good agreement with the assumption that the trichobothria's function resides in the localization of prey (cf. preceding paper). They do not permit any statements about whether the trichobothria are used for the perception of wind direction as well (cf. Linsenmair, 1968).

4. Directional Sensitivity

The cosine-like dependency of the receptor response on the azimuthal angle of hair deflection (Fig. 10) might possibly be connected with mechanical processes in the auxiliary structures: compression of the tubular body will, presumably, be found at a defined stimulus direction only (cf. Görner, 1965; Christian, 1971, 1972). The biological consequence of the directional sensitivity dependency described resides in the trichobothria's capability of discriminating different stimulus directions (Görner, 1965; preceding paper). Since there is multiple innervation in the trichobothria two organs would, theoretically, suffice for prey localization in space. Since more than two organs, however, will simultaneously be excited by the air movements a convergent connection of several receptor channels seems to be likely.

The present paper is part of a doctoral thesis. My thanks are due to Prof. Dr. P. Görner for the theme, many valuable discussions and his constant readiness to help.

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